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REPRODUCTIVE SUCCESS OF CANADA GEESE: IMPLICATIONS OF THE VARIATION IN EGG SIZE

by

YVES LEBLANC

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled REPRODUCTIVE SUCCESS OF CANADA GEESE: IMPLICATIONS OF THE VARIATION IN EGG SIZE submitted by YVES LEBLANC in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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Abstract

The impact of variation in egg size on a series of reproductive parameters in Canada geese (*Branta canadensis*) was investigated. Data were collected from eggs of wild and captive Canada geese to document the variation in size. Goslings were marked at hatching and recaptured near fledging to determine the effects of egg size on the reproductive success of females and the survival of goslings.

Most variation (60%) in fresh egg mass and index of egg volume was explained by differences among females. Multiple correlation analysis revealed a positive but weak relationship between mean egg size and female condition. High indices of repeatability obtained with captive females suggested that genetic differences might explain a large part of the differences among females. These differences did not affect the number of goslings that reached fledging age.

Variation of size among eggs within a clutch accounted for a third of the total variance in size. Eggs in the middle of the sequence were very similar, yet larger than the first and last egg of the sequence. Undetermined physiological changes in the reproductive tract at the onset and termination of laying may explain this consistent pattern of variation within clutches.

The mass of goslings at hatching was strongly correlated with fresh egg mass. Differences in the size and position in the laying sequence of eggs within a clutch did not affect their hatching success and the fledging success of the gosling. From these results, I concluded that egg size had a very weak effect on the "fitness" of a female or the chick produced.

Additionally, there was no evidence that female Canada geese invested more in one sex of gosling than the other. This conclusion was based on the fact that position in the laying sequence, egg mass, and hatching mass did not differ between male and female goslings.

Résumé

Cette étude a porté sur la variabilité de la grosseur des oeufs de bernache du Canada (*Branta canadensis*) et l'effet de celle-ci sur le succès reproducteur des femelles et la survie des oisillons. Les données ont été recueillies à partir d'une population nichant dans le sud-est de l'Alberta et d'un groupe d'individus gardé en captivité. Les oisillons ont été marqués à l'éclosion et recapturés lorsqu'ils étaient âgés de cinq à huit semaines.

Soixante pour cent de la variance calculée dans la grosseur des oeufs était attribuable aux différences entre les femelles. L'indice lipidique des femelles était faiblement, mais significativement corrélé avec la grosseur des oeufs. Ces différences pourraient être causées en majeure partie par des différences génétiques entre les femelles. En effet, celles qui ont produit plus d'une couvée, ont pondu des oeufs de grosseur similaire. Ces différences dans la grosseur des oeufs entre les femelles n'ont cependant pas influencé le taux de recapture de leurs oisillons.

Environ 30% de la variabilité de la grosseur des oeufs était causé par des différences présentes à l'intérieur d'une même couvée. Les premiers et les derniers oeufs de l'ordre de ponte étaient les plus petits de la couvée alors que ceux du milieu étaient les plus gros et très similaires entre eux. Ces différences n'ont cependant pas affecté le taux d'éclosion et le taux de recapture des oisillons. J'ai donc conclu d'après ces résultats que la grosseur de l'oeuf a très peu d'effets sur le succès reproducteur des femelles et sur la survie des jeunes.

De plus, des données recueillies sur le sexe des oisillons ont révélé que les femelles n'ont pas investi plus de ressources énergétiques dans un oisillon de sexe mâle ou femelle. Cette conclusion est basée sur l'absence de différences entre les oisillons mâles et femelles de la masse de l'oeuf, la masse à l'éclosion, la longueur du culmen et du tarsus.

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I. INTRODUCTION

In many studies of avian species, "fitness" has been estimated using either the number of eggs produced or the number of chicks reaching fledging age. The factors that cause and maintain variation in clutch sizes among individuals of the same species or among different species have received considerable attention (e.g., Lack 1967, Klomp 1970, Ricklefs 1977, Winkler and Walters 1983). However, unlike clutch size variation, egg size variation has not been at the centre of interest for avian evolutionary ecologists apart from the recent work of Ojanen (1983). As a result, little information is available on the causes of variation of egg size and its potential influence on the relative "fitness" of the chick produced from or the female producing eggs.

Like clutch size, egg size varies considerably among individuals of the same species (e.g., Lack 1968, Vaisanen et al. 1972, Ankney and Bisset 1976, Manning 1978) and among different populations of the same species (e.g., Batt and Prince 1978, Manning 1978, Miller 1979, Otto 1979). Variation in egg size may reflect differences in the age (e.g., Coulson 1963, Cooper 1978, Mills 1979), in body size (Otto 1979), and in body condition of females (Jarvinen and Vaisanen 1984). Recent findings by Ojanen et al. (1979) and van Noordwijk et al. (1981), however, support the idea that a major part of the variation observed in egg size among females reflects genetic differences among them.

The reproductive success (estimate of fitness) of females producing larger eggs has been shown to be higher in herring gulls (*Larus argentatus*) (Parsons 1970), great tits (*Parus major*) (Schifferli 1973), and European swifts (*Apus apus*) (O'Connor 1979). In controlled experiments, larger chicks from larger eggs survived better than smaller chicks from smaller eggs (Ankney 1980, Moss et al. 1981, Rhymer 1982). Larger lipid reserves (Parsons 1970), better energetic and physiological advantages (Kendeigh 1960, Rhymer 1982), and a more advanced stage of development (Schifferli 1973) are the main reasons invoked in the discussion of the advantages of hatching from an egg

of larger size. Variation of egg size within a clutch may have an adaptive value (see Slagsvold et al. 1984, for a discussion of this topic). Within a clutch, male offspring tended to be produced in large and first eggs of snow geese (Ankney 1982, but see Cooke and Harmsen 1983).

In light of these findings, I report in this thesis, the results of a study of egg size variation of wild and captive Canada geese (*Branta canadensis*) nesting at mid latitudes. This species was selected for three reasons. First, nests are easily located and their eggs readily measured. Second, a breeding population of captive birds held in the same area where wild birds were nesting offers a valuable opportunity for comparative studies. Moreover, captive birds can be handled throughout their reproductive cycle without any apparent trauma. Third, an extensive body of information on the biology of this species is available (see Cooper 1978, and references therein).

The aim of my research was to quantify the sources and to determine the causes of variation in egg size, and to examine the effect of this variation on the reproductive success of Canada geese, as estimated by the number of goslings fledged.

In this thesis, I present the results in three chapters. The first (Chapter II) deals mainly with the question of the causes of variation in egg size of Canada geese. Quantitative analyses are presented and discussed in relation to other studies of the same and other species. The second (Chapter III) addresses the question of whether egg size has any effect on the reproductive success of geese. Along with this, is a study of the effects of 1) position in the laying sequence and 2) brood size on the reproductive success. The third (Chapter IV) addresses the question of whether females invest more in goslings of one sex than the other. Though not directly related to the point of egg size variation, this information is relevant when one considers the variation of egg size within clutches of Canada geese.

Lastly, I integrate my results with those of other studies and discuss the value of egg size as an estimate of lifetime reproductive output.

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II. EGG SIZE VARIATION IN CANADA GEESE

INTRODUCTION

Lack (1967, 1968) suggested that, among the members of the Anatidae, the amount of food available to females and/or body reserves carried by them could be diverted to either few large or many small eggs. He noted that egg size was relatively constant within each species of Anatidae, and suggested that differences between species existed because of hereditary factors, thus in each species, egg size would have evolved as a compromise between the provisioning of sufficient nutrients within each egg to assure survival of the chick and reducing the number of eggs produced per clutch.

Lack (1968) found a wide range of egg mass in emperor (*Aptenodytes forsteri*) and king penguins (*A. patangonicus*). He postulated that because these species of penguins could lay only one egg, they could modify only egg size, not clutch size. Likewise, Ankney and Bisset (1976) reported a large range of variation of fresh egg mass in a population of snow geese (*Chen caerulescens*). The range in size, used as a measure of variation, was reported to be large also in Canada (*Branta canadensis*; Manning 1978) and greylag geese (*Anser anser*; Young 1964, 1972).

Internal and external factors such as age of the female, body size, body condition, and laying sequence may increase variation of egg size within a species (e.g., Romanoff and Romanoff 1949, Coulson 1963, Kear 1965, Parsons 1976, Myrberget 1977, Miller 1979, Mills 1979, Otto 1979, Houston et al. 1983, Jarvinen and Vaisanen 1984). However, recent studies have suggested that egg size might have a strong heritable component (e.g., Ojanen et al. 1979, van Noordwijk et al. 1981).

The first objective of this study was to document the amount of variation in the characteristics of eggs produced by a population of Canada geese (*B. c. moffiti*) nesting at mid latitude. Different measures of variability were used and compared to previous studies of the same and other species. The second objective was to quantify the relative contribution to the total

variation recorded from that 1) within clutches, 2) among clutches (females), 3) among years, and 4) among areas. The third objective was to investigate possible causes of phenotypic variation observed in egg size.

STUDY AREA AND METHODS

I conducted my study during the summers of 1983 and 1984. I collected data from two different sources: a breeding population of wild Canada geese and a breeding flock of captive birds maintained at the Brooks Wildlife Center, Alberta.

Captive Canada geese

Data were available from 34 pairs in 1983 and 21 pairs in 1984, of which 19 pairs were common to both years. All females, with the exception of two, originated from a breeding population of wild geese in the vicinity of Brooks, Alberta (D.E. Hofman, pers. comm.).

In late March of each year, pairs from the captive flock were released into alleyways that gave access to a series of contiguous breeding pens. Each breeding pen had wire mesh walls and ceiling and was 10 X 10 X 1.3 m high and enclosed a 2.6 X 2.6 m pond, a metal feeder, and a nesting structure. Once a pair was seen defending the same pen for 1 or 2 days, it was isolated from other birds by closing the access door to the alleyway.

From April 1 to May 30, I checked every pen daily for new eggs. I marked with a waterproof felt pen each new egg on the date of discovery and weighed it with a spring scale of 300 g capacity calibrated in 2 g intervals. Maximum length and breadth of each egg were measured with Vernier calipers and recorded. In 1983, to induce renesting, I removed the entire clutch 5 days after the date of laying of the last egg. In 1984, I removed the completed clutch earlier (3 days after the laying of the last egg) in a attempt to increase the number of renesting attempts (Sowls 1955). Each year, on the day of clutch removal, I weighed the female with a 5-kg Pesola spring scale calibrated in 0.1 kg intervals, and recorded the tarsus and culmen

lengths. In 1984, I also determined the wing chord length. In addition to these measurements, four others were obtained in February 1985 for all females that bred in 1984. They were head length, culmen length at gape, length of the ninth primary (from point of insertion of calamus to tip), and the diameter of the ninth primary at the superior umbilicus. I used these data to determine an index of size using an analysis of principal components.

Wild Canada geese

This study was conducted near Brooks (50° 35' N, 111° 54' W) in the shortgrass ecoregion of southeastern Alberta (Strong and Leggat 1981). In 1983, I studied four reservoirs: Gleddie Lake, Tilley "A", Tilley "B", and Rolling Hills Lake (Fig. II-1). In 1984 my study area included two additional reservoirs: Kininvie Flat and Cowoki Lake (Fig. II-1). All reservoirs were located within a circle of 16 km radius. The shortest and longest distances between 2 reservoirs were 1 and 32 km respectively.

Mean daily temperatures for April and May recorded by Environment Canada for Brooks for 1983 were 4.8°C and 10.5°C and for 1984, 6.3°C and 10.3°C respectively.

The population of Canada geese nesting on the study site has been increasing for several years and its expansion throughout southeastern Alberta has not been affected apparently by the recent drought (D.E. Hofman, pers. comm.).

In 1983 and 1984, I collected data from 123 and 222 complete clutches produced in the wild. In 1983, I searched Gleddie Lake daily for nests from late March to late April. All other reservoirs were checked every 3 or 4 days in 1983. The following year, I visited Gleddie Lake every 2 days and all other areas every 2 to 4 days.

Upon discovery, the location of a nest was recorded on a map of the lake. Each egg was marked with a waterproof felt pen with the date of discovery. Sequence of laying was determined by the degree of soiling of the egg (Cooper 1978) only in nests with three eggs or less. Mass,

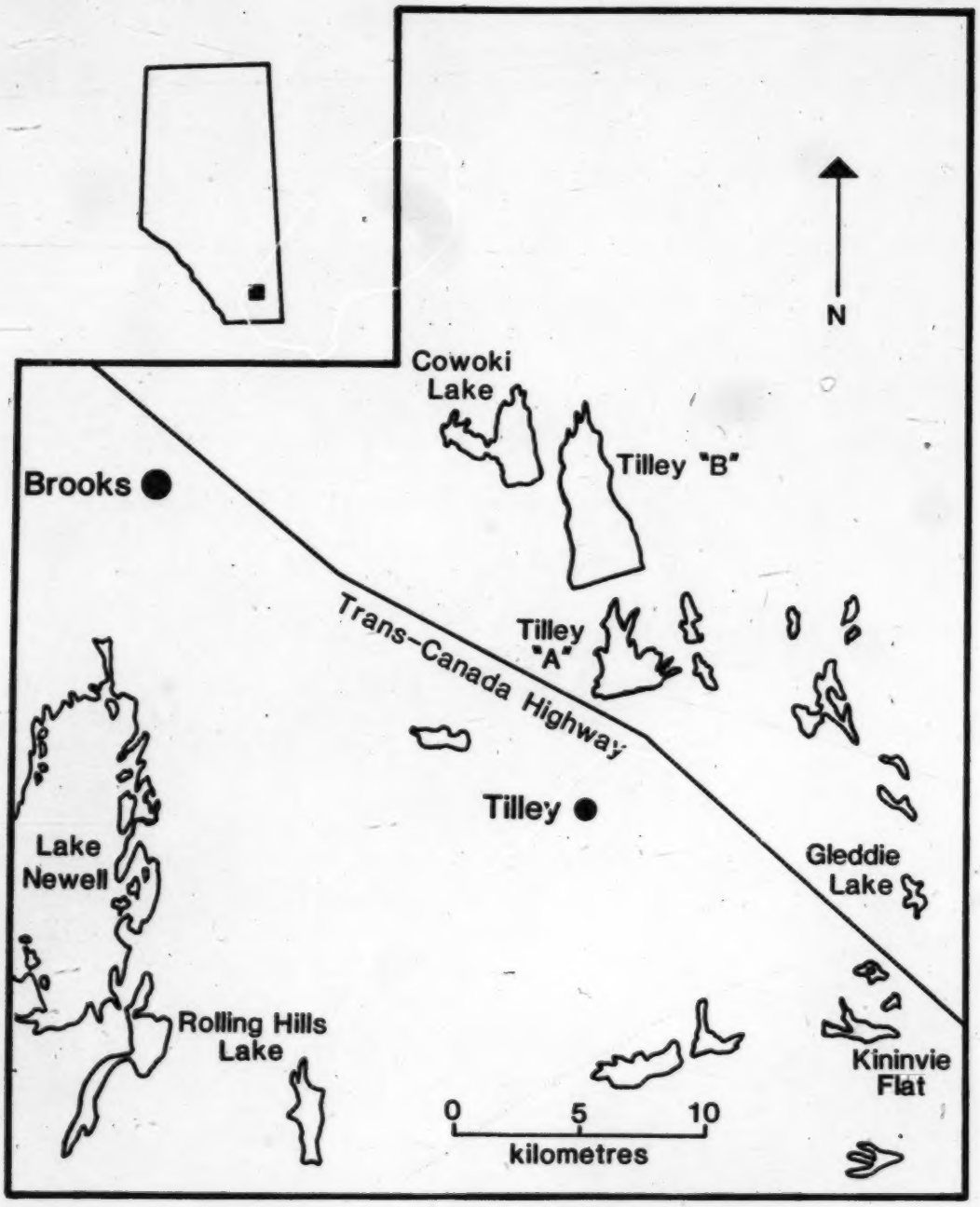

Figure II-1: Location of the study area in Southeastern Alberta in 1983 and 1984.

maximum length and breadth were determined for each egg. Subsequent visits every 2 or 3 days during laying period allowed me to determine the laying sequence of the rest of the clutch.

To keep disturbance of the nesting areas to a minimum level, I revisited many nests near completion, only about midway through incubation. To estimate the fresh mass of eggs laid after the previous visit, I added a value of 1 g/day of incubation to compensate for the loss in mass incurred in the interval. This value was obtained by plotting average loss of mass for 52 clutches during incubation (Fig. II-2). In most clutches in which this correction had to be made, it concerned only the last one or two eggs laid in the clutch. I believe that this correction did not affect my results significantly.

No attempts were made to estimate the fresh egg masses of completed clutches found during incubation. An index of volume was used as a alternative estimator of egg size. It was calculated using the formula: length X breadth^2. Using only one egg per clutch, I plotted fresh egg mass against its index of volume (Fig. II-3). Index of volume was found to be a good estimator of fresh egg mass.

The laying of the first egg in a nest, herein referred as the date of laying, was estimated in 89% of the completed nests (N = 345). Three methods were used to determine date of laying. The first one was used when the nest was found during laying. The time to lay a given number of eggs was subtracted from the date of discovery. Because the average time between laying of two consecutive eggs was 1.55 days (SD = 0.33, N = 140 clutches), an odd number of eggs would require a given number of days plus half of an another day. However to get a integer value for date of laying, I used the integer number before and after the fractional time calculated, in an alternate sequence for nests with odd numbers of eggs. For example, if three nests contained three eggs each, I would assign 5 days to the first, 4 days to the second, and 5 days to the third as the time required to lay the clutch. I used a second method for 21 clutches. The hatching date, which was defined as the first day that any egg was observed pipping

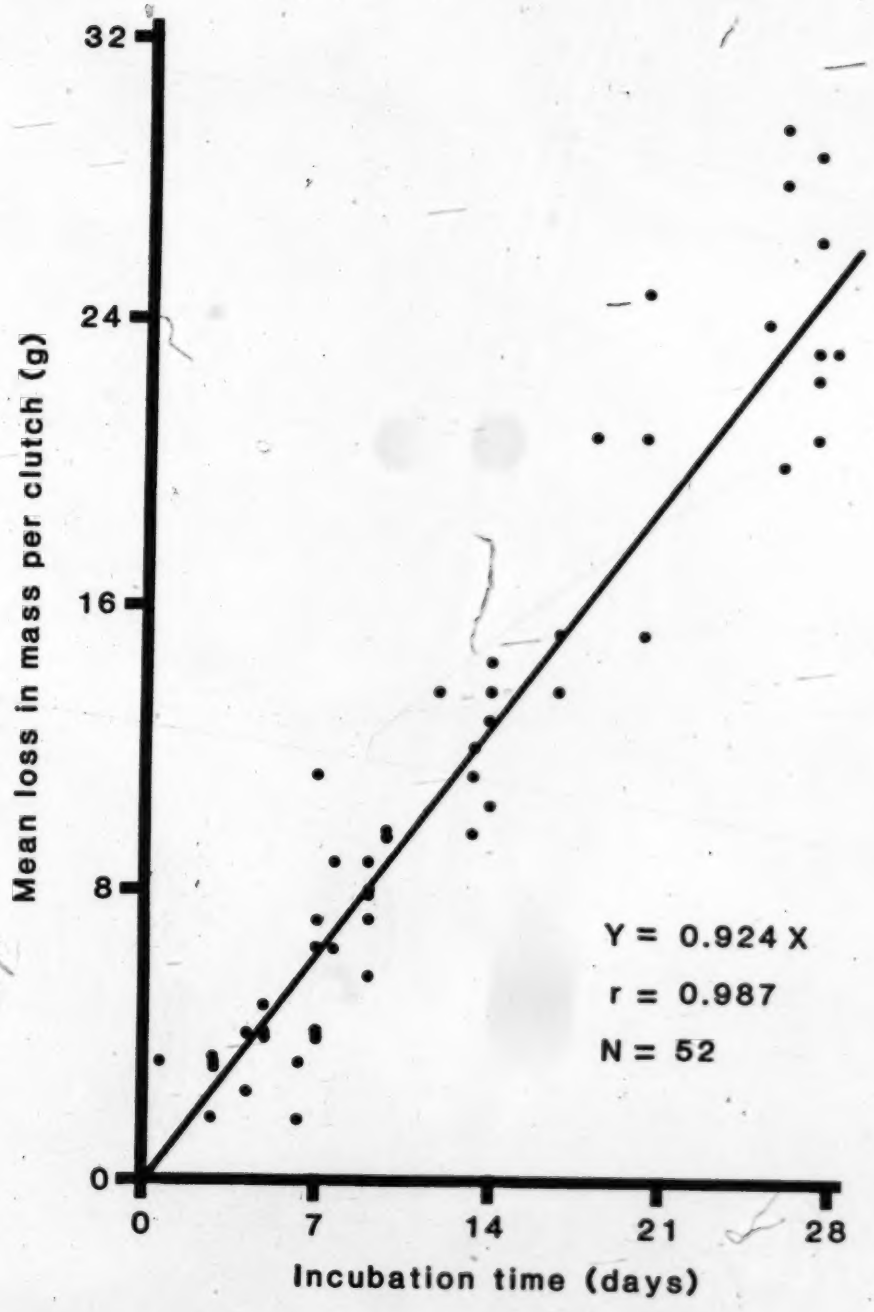

Figure II-2: Relationship between mass and days of incubation for the eggs of wild Canada geese.

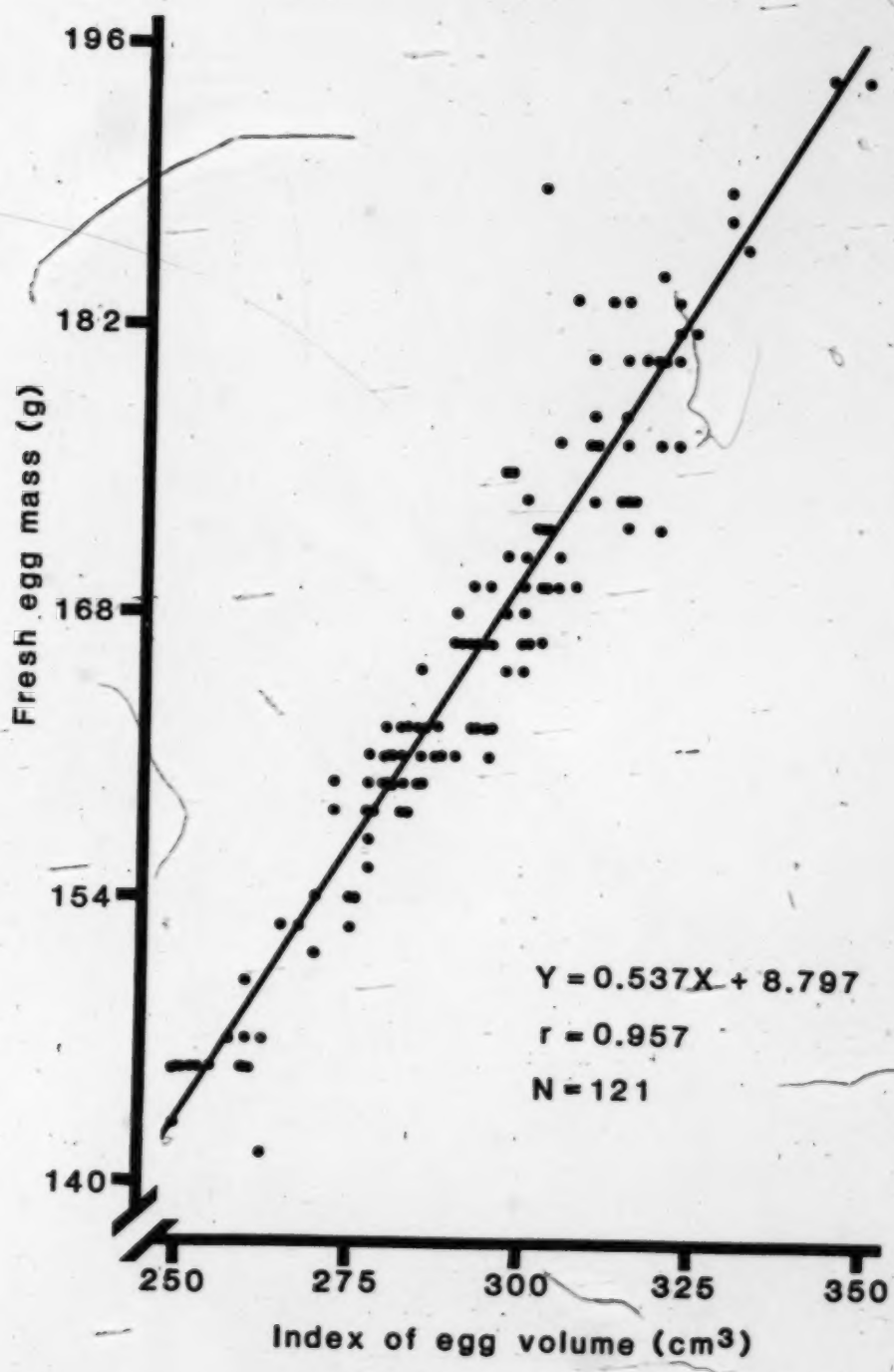

Figure II-3: Relationship between fresh egg mass and index of volume (length X breadth²) for clutches (one egg per clutch) of wild Canada geese nesting at Brooks, Alberta.

(Finney and Cooke 1978), was known in these clutches. To obtain the date of laying, I subtracted a round figure of 27 days ($\bar{X}$ = 26.9, SD = 1.1, N = 53) for incubation time plus the appropriate time to lay all eggs. I tested this method on 39 clutches for which laying date were known (nests found with only one egg or two eggs) by plotting the estimated value against the observed value. The coefficient of determination (r^2) was 0.965. A third method was used for estimating laying date in 51 clutches. Because egg density decreases as the incubation advances, knowing the density permits one to estimate incubation time. In my study, index of density, defined as mass/index of volume, was negatively correlated with incubation time (Fig. II-4). Having obtained the incubation time from the equation, I then subtracted this number of days plus that for laying the number of eggs in the clutch from the date of discovery of the nest. I tested this method on 40 nests with known laying dates. Of all estimated values, 77% were within ± 3 days of their known values.

Coefficients of variation were compared using the technique of Sokal and Braumann (1980). Analysis of variance followed the procedures of Sokal and Rohlf (1981) and they were done using the SPSSx (SPSSx Inc. 1983) statistical package.

RESULTS

Range in size of eggs and coefficient of variation

Two indices of variation in size were calculated for eggs of captive and wild birds. Their relative value as indicators of phenotypic variation were compared.

Range, coefficient of variation (CV), and other descriptive statistics of mean egg mass per clutch (MEM) and mean index of volume per clutch (MIV) of Canada geese in captivity are given in Table II-1 and in the wild in Table II-2. No differences were found between years in values of the CV for either the captive or wild birds ($P > 0.05$). Coefficients of variation of MEM

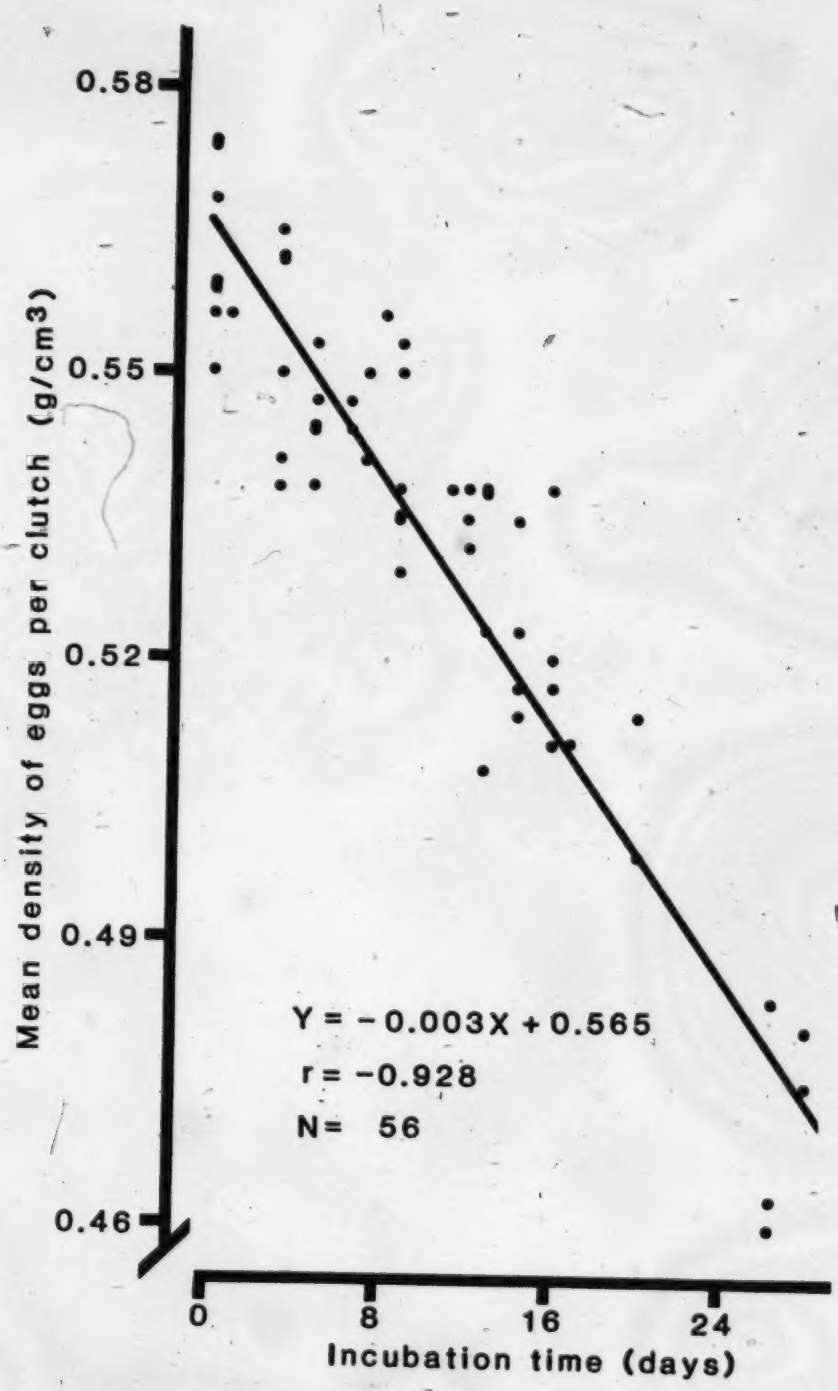

Figure II-4: Relationship between the mean density of eggs per clutch and incubation time.

TABLE II-1: Egg size characteristics of a population of Canada geese held in captivity at Brooks, Alberta.

Characteristics	Year	$\bar{X}$±SD	N	CV	Range
Egg mass (g)	1983	161.6±10.5	183[1]	6.50	136.0-188.0 (72.3)[2]
	1984	163.0±11.7	118[1]	7.19	132.0-186.0 (71.0)
Index of egg volume (cm^3)	1983	288.0±18.9	183[1]	6.56	240.2-332.0 (72.4)
	1984	286.4±20.6	118[1]	7.21	231.4-329.0 (70.3)
Mean egg mass per clutch (g)	1983	161.9± 9.5	34[3]	5.91	140.8-185.0 (76.1)
	1984	163.0±10.2	21[3]	6.34	137.5-182.5 (76.4)
Mean index of egg volume per clutch (cm^3)	1983	288.5±17.1	34[3]	5.98	245.0-328.7 (74.5)
	1984	286.3±18.0	21[3]	6.35	245.5-321.2 (76.4)

[1] No. of eggs
[2] Ratio of the minimum value to the maximum X 100
[3] No. of clutches

TABLE II-2: Egg size characteristics of a population of wild Canada geese at Brooks, Alberta.

Characteristics	Year	$\bar{X}$±SD	N	CV	Range
Egg mass (g)	1983	161.9±12.0	343[1]	7.43	131.0-195.0 (67.2)[2]
	1984	164.3±11.9	1073[1]	7.26	129.0-200.0 (64.5)
Index of egg volume (cm^3)	1983	290.5±20.5	487[1]	7.06	232.1-351.4 (66.1)
	1984	290.1±21.5	1214[1]	7.41	227.2-374.2 (60.7)
Mean egg mass per clutch (g)	1983	162.2±10.2	60[3]	6.33	144.2-186.2 (77.4)
	1984	164.4±10.6	189[3]	6.44	137.5-194.8 (70.5)
Mean index of egg volume per clutch (cm^3)	1983	291.0±17.7	84[3]	6.11	252.8-333.9 (75.7)
	1984	290.1±18.6	216[3]	6.43	243.0-342.9 (68.2)

[1] No. of eggs
[2] Ratio of the minimum value to the maximum X 100
[3] No. of clutches

and MIV of captive geese were not statistically different from those of wild geese ($P > 0.50$). For each completed clutch in captivity and in the wild, I calculated the within-clutch CV of egg mass and index of volume. In captivity, the mean CV of egg mass and the mean CV of index of volume were 3.5% and 3.5% in 1983, and 4.1% and 4.0% in 1984. In the wild, they were respectively 4.2% and 4.0% in 1983 and, 4.0% and 3.9% in 1984. No differences were found between the 2 groups for either egg mass or index of volume in 1983 (mass: t-test, $t = 1.846$, $DF = 92$, $P = 0.07$; index of volume: $t = 1.409$, $DF = 116$, $P = 0.16$) and 1984 (mass: $t = 1.111$, $DF = 209$, $P = 0.27$; index of volume: $t = 0.265$, $DF = 236$, $P = 0.79$).

Components of variance in egg characteristics

The proportion of the total variance attributable to experimental errors was investigated for length, breadth, and index of volume using three repeated measurements of 14 eggs. An analysis of variance revealed that only 0.04%, 0.11%, and 0.06% of the total variance (among eggs + among repeated measurements of the same egg) for length, breadth, and index of volume respectively, was accounted by experimental errors. Therefore, their contributions to the total variance appear to be minimal.

Variation among clutches (females) in the characteristics of eggs of captive Canada geese accounted for approximately three-fifths of the total variance in mass, length, breadth, and index of volume (Table II-3). Variation in egg characteristics of successive clutches of the same female explained very little of the total variance recorded for egg characteristics. Variation within clutches accounted for about one-third of the total variance in mass, length, and index of volume. The variation in breadth within clutches was relatively greater than any other characteristics.

The variation among clutches of wild Canada geese laid the same year or in 2 consecutive years by the same female, could not be estimated because females were not marked. As in captivity, however, most of the variation in the characteristic of the egg was accounted for by differences

TABLE II-3: Analysis of variance of egg dimensions from a captive flock of Canada geese held at Brooks, Alberta.

Source of variation	DF	Mean squares	Variance component	Percentage variability
Egg mass				
Among clutches of different females	35	909.1	75.02	62.9
Among clutches of a given female	40	57.2	3.00	2.5
Among eggs within a clutch	336	41.2	41.19	34.6
Egg length				
Among clutches of different females	35	77.4	6.22	60.5
Among clutches of a given female	40	6.8	0.60	5.8
Among eggs within a clutch	336	3.5	3.47	33.7
Egg breadth				
Among clutches of different females	35	12.7	0.99	55.0
Among clutches of a given female	40	1.4	0.12	6.7
Among eggs within a clutch	336	0.7	0.69	38.3
Index of egg volume				
Among clutches of different females	35	2824.9	229.48	62.1
Among clutches of a given female	40	221.4	18.22	4.9
Among eggs within a clutch	336	121.7	121.72	33.9

among and within clutches (Table II-4). Differences between years appeared to be nonexistent in all characteristics except mass which explained only 5% of the variance. Differences between sites explained less than 4% of the total variance.

Factors influencing variation of egg characteristics

Variation of egg characteristics within clutches

I tested the effect of egg sequence on egg characteristics using data from the captive flock and a two-way ANOVA without replication (Sokal and Rohlf 1981). For this design, the assumption that no interaction exists between sequence and clutches must be made (Sokal and Rohlf 1981). I tested the validity of this assumption using data collected from 9 females that laid 6 eggs in 2 clutches either the same year or in 2 different years in captivity. No significant interaction term was found for any of the characteristics (range of P values= 0.457-0.769). In other words, the pattern of variation of egg characteristics is consistent among different clutches.

There were significant associations between mass, length, breadth, and index of volume of an egg and its position in the laying sequence in clutch sizes of 5, 6, and 7 (Table II-5). The small sample of clutches of 4 eggs laid in captivity might explain the lack of statistical significance of the effect of laying sequence in this clutch size because the trend was similar to that of larger clutches (Table II-5).

The effect of position in the laying sequence of eggs produced in the wild was analysed with the same design as those from the captive birds. Only clutches for which laying sequence was known (see STUDY AREA AND METHODS) were used in this analysis. As with captive birds, egg characteristics were associated significantly with laying sequence for all clutch sizes (Table II-6). In addition, descriptive statistics of each characteristic were plotted in Figures II-5 to II-8.

TABLE II-4: Analysis of variance of egg dimensions from a wild population of Canada geese breeding near Brooks, Alberta.

Source of variation	DF	Mean squares	Variance component	Percentage variability
Egg mass				
Among sites	4	2193.7	0.45	0.31
Among years	3	1468.5	7.29	5.01
Among clutches	242	582.8	95.39	65.58
Among eggs within a clutch	1166	42.3	42.32	29.10
Egg length				
Among sites	4	143.6	0.33	3.01
Among years	3	36.7	0.00	0.00
Among clutches	295	40.9	6.54	59.62
Among eggs within a clutch	1402	4.1	4.10	37.38
Egg breadth				
Among sites	4	25.2	0.06	2.55
Among years	3	6.3	0.00	0.00
Among clutches	295	9.3	1.52	64.68
Among eggs within a clutch	1402	0.8	0.77	32.77
Index of egg volume				
Among sites	4	6885.3	16.78	3.68
Among years	3	1583.9	0.00	0.00
Among clutches	293	1806.3	294.23	64.54
Among eggs within a clutch	1400	144.9	144.87	31.78

TABLE II-5: Relationship between position in the laying sequence and size characteristics of eggs of captive Canada geese. Values in the table are F values based on a two-way ANOVA without replication.

Characteristics	Clutch size			
	4 (7)[1]	5 (16)	6 (27)	7 (4)
Egg mass	2.75	11.40***	15.35***	4.31*
Egg length	1.34	4.57**	3.86**	2.35*
Egg breadth	0.38	9.71***	61.14***	4.32*
Index of egg volume	1.38	10.26**	10.80***	3.56*

[1] No. of clutches
* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

TABLE II-6: Relationship between position in the laying sequence and size characteristics of eggs of wild Canada geese breeding near Brooks, Alberta. Values in the table are F values based on a two-way ANOVA without replication.

Characteristics	Clutch size			
	4[1]	5[2]	6[3]	7[4]
Egg mass	6.26**	9.60**	21.11***	6.50***
Egg length	2.44	2.45*	3.84**	1.75
Egg breadth	2.47	2.86*	14.44**	3.99**
Index of egg volume	4.97**	4.49**	14.61***	3.34**

[1] DF for all characteristics: 3,30
[2] DF for egg mass: 4,196; other characteristics: 4,176
[3] DF for egg mass: 5,196; other characteristics: 5,248
[4] DF for egg mass: 6,96; other characteristics: 6,90
* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

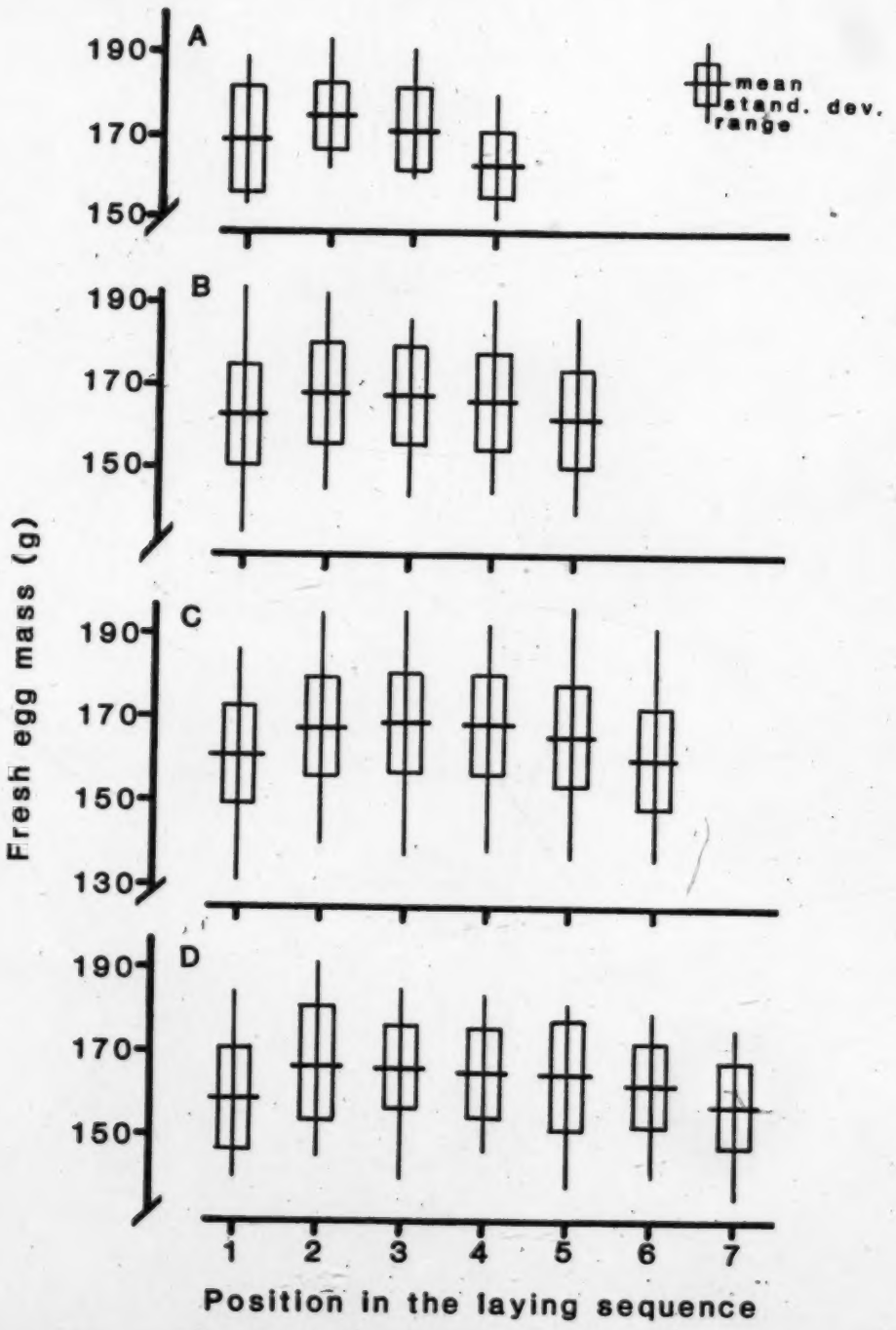

Figure II-5: Relationship between the fresh mass of an egg and its position in the laying sequence. A) four-egg clutches, B) five-egg clutches, C) six-egg clutches, and D) seven-egg clutches.

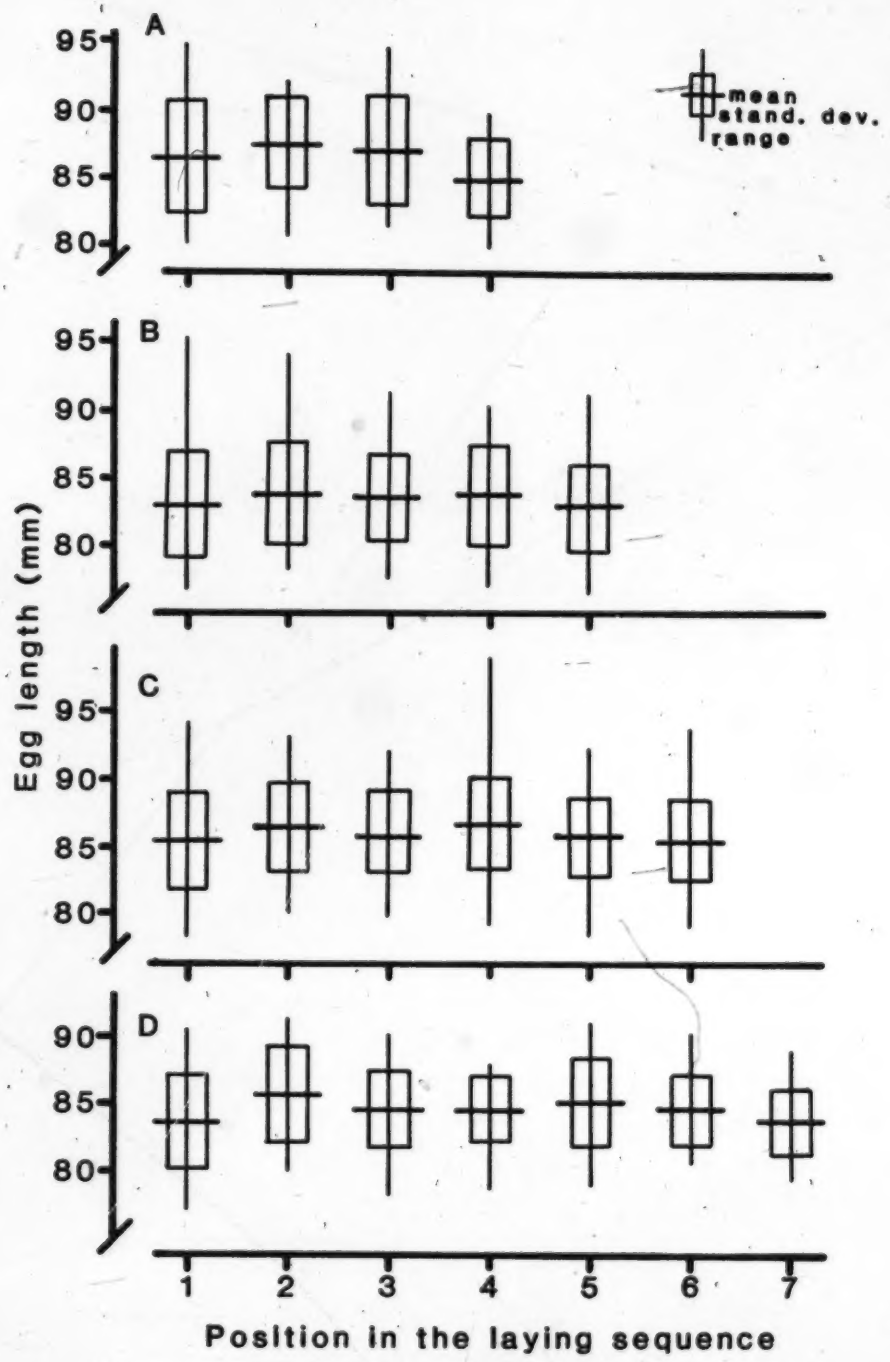

Figure II-6: Relationship between the length of an egg and its position in the laying sequence. A) four-egg clutches, B) five-egg clutches, C) six-egg clutches, and D) seven-egg clutches.

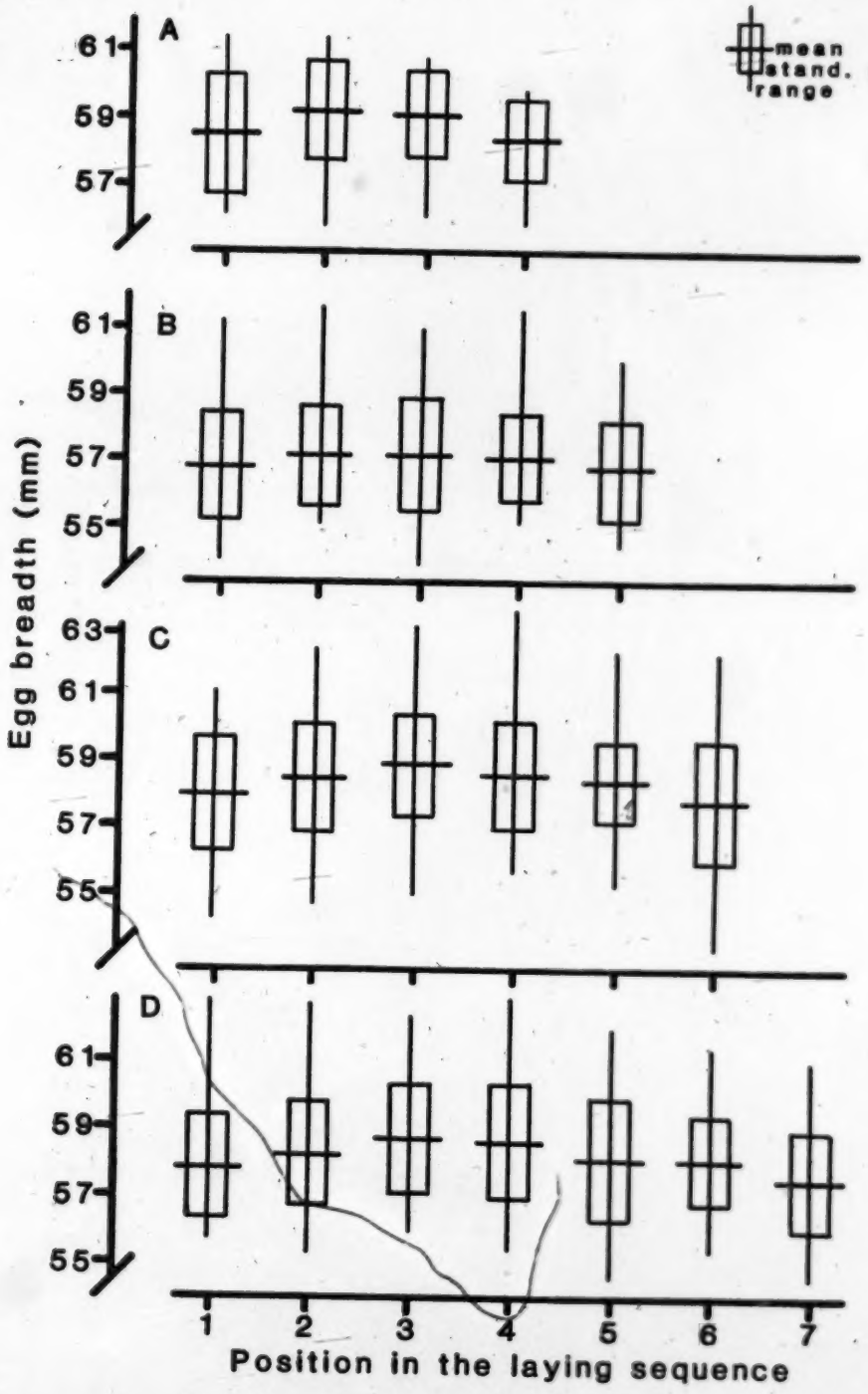

Figure II-7: Relationship between the breadth of an egg and its position in the laying sequence. A) four-egg clutches, B) five-egg clutches, C) six-egg clutches, and D) seven-egg clutches.

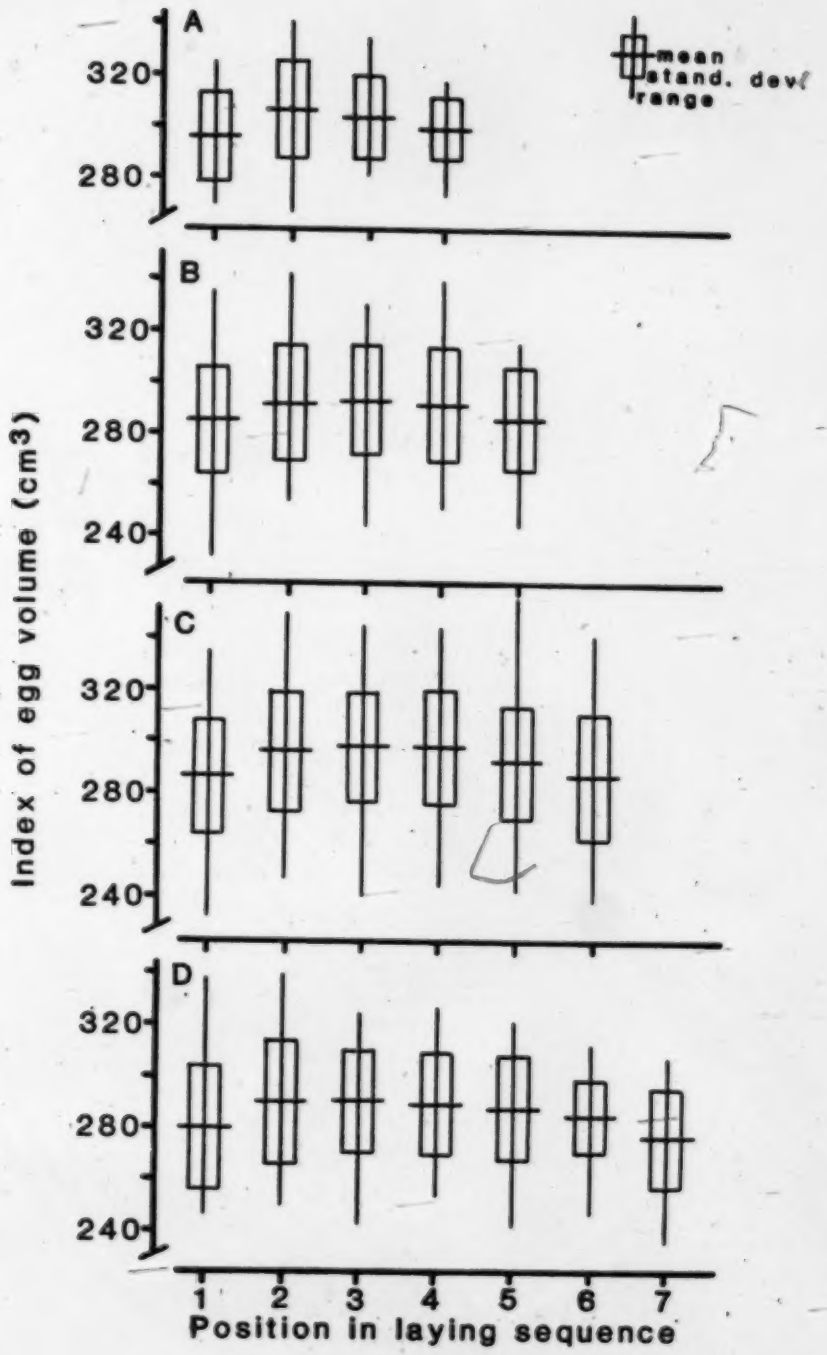

Figure II-8: Relationship between the index of volume (length X breadth²) of an egg and its position in the laying sequence. A) four-egg clutches, B) five-egg clutches, C) six-egg clutches, and D) seven-egg clutches.

All clutch sizes investigated showed a common pattern of variation in mass and index of volume according to the position of the egg in the laying sequence. These characteristics followed a curvilinear pattern with eggs in the middle of the sequence being very similar in mass, yet larger than the first and last eggs in the sequence.

On average, the lightest egg in a clutch weighed 91.0% (no. of clutches = 250) of the heaviest egg. The index of volume of the smallest egg was also 91.0% (no. of clutches = 301) of the largest egg of the clutch. No difference in mass between the first and last egg of a clutch was found (paired t-test: $t = 1.470$, $df = 127$, $P = 0.14$).

Variation of egg characteristics among clutches

Using each year's data on egg characteristics from the captive flock, I did a multiple correlation analysis to test the influence of certain variables on MEM and MIV, namely: age of the female, date of laying, clutch size, index of condition, and index of body size. The index of condition, defined here as body mass over tarsus length, was the best estimator of total fat reserves available in my study (see Gauthier and Bédard 1985). In 1983 and in 1984, the index of condition explained a significant part of the variance in MEM and MIV (Tables II-7 and II-8). There was slight statistical evidence in 1984 that age of the female was correlated with egg size. However, the trend was opposite to that of 1983.

As with eggs produced in captivity, I tested if date of laying and clutch size of egg produced in the wild were significantly correlated with MEM and MIV using a multiple correlation analysis. In 1983 I pooled all data from all areas because there were no statistical differences among areas in either MEM or MIV (Table II-9). In 1983, neither date of laying nor clutch size were significantly correlated with MEM or MIV. In 1984, I did the analysis for each area separately because there were significant differences among areas in egg size (Table II-9). MIV was negatively correlated with date of laying at Gleddie Lake ($r = -0.321$, $df = 38$, $P = 0.04$). No other

TABLE II-7: Multiple correlation analysis of selected biological variables on mean egg mass per clutch of captive Canada geese.

Variables	Year	Partial correlation coefficient	N	P
Index of condition	1983	0.415	32	0.007
	1984	0.418	19	0.030
Age of the female	1983	0.110	30	0.275
	1984	-0.369	18	0.055
Clutch size	1983	-0.154	32	0.192
	1984	0.044	19	0.425
Date of laying	1983	0.117	32	0.255
	1984	-0.281	19	0.108
Index of body size	1983	-0.034	32	0.425
	1984	-0.150	19	0.258

TABLE II-8: Multiple correlation analysis of selected biological variables on mean index of egg volume per clutch of captive Canada geese.

Variables	Year	Partial correlation coefficient	N	P
Index of condition	1983	0.399	32	0.010
	1984	0.425	19	0.027
Age of the female	1983	0.067	30	0.357
	1984	-0.364	18	0.057
Clutch size	1983	-0.137	32	0.219
	1984	0.039	19	0.433
Date of laying	1983	0.106	32	0.276
	1984	0.175	19	0.224
Index of body size	1983	-0.073	32	0.341
	1984	-0.313	19	0.083

TABLE II-9: Egg sizes of wild Canada geese breeding near Brooks, Alberta in different areas in 1983 and 1984. Values in the table are mean ± 1 standard deviation.

Area	Mean egg mass (g)			Mean index of volume (cm^3)		
	1983	1984	P[1]	1983	1984	P[1]
Gleddie Lake	163.1±10.3 (36)[2]	168.7±10.0 (40)	0.021	292.7±17.9 (45)	294.9±18.8 (43)	0.586
Rolling Hills Lake	156.2±9.3 (3)	162.6±10.3 (63)	0.290	292.2±15.6 (21)	287.4±17.9 (75)	0.265
Tilley "A"	162.5±9.9 (18)	160.3±9.9 (26)	0.466	284.4±20.5 (12)	283.0±18.7 (25)	0.838
Tilley "B"	154.3±11.4 (3)	---------- ---	-----	287.4±18.9 (6)	---------- ---	-----
Kininvie Flat	---------- ---	168.4±12.3 (25)	-----	---------- ---	297.3±20.9 (29)	-----
Cowoki Lakes	---------- ---	162.9±8.8 (35)	-----	---------- ---	289.6±16.0 (44)	-----
P[3]	0.379	0.002	-----	0.491	0.013	----

[1] Based on a t-test comparing years
[2] No. of clutches
[3] Based on a oneway ANOVA comparing areas

significant relationships were found between the other biological variables and with either MEM or MIV. The large differences in MEM among females in the wild population resulted in a considerable overlap of total clutch mass among clutches of different size (Fig. II-9). For example, the total clutch mass of 49% of all 5-egg clutches was greater than that of the lightest 6-egg clutch, and among 6-egg clutches, 43% of them were heavier than the lightest 7-egg clutch.

Variation of egg characteristics among years

Mean masses and mean indices of volume of eggs within a clutch did not differ among years in captivity ($P = 0.50$). For 19 females that laid one clutch in both years, there were no differences between years in any egg characteristic (Table II-10). Descriptive statistics of MEM and MIV for each area are given in Table II-9. Only at Gleddie Lake was mean MEM in 1984 significantly greater than in 1983. No differences between years were found at either Tilley "A" or at Rolling Hills Lake.

Variation of egg characteristics among areas

In 1983, I found no significant differences among areas in mean MEM or mean MIV (Table II-9). However, in 1984, MEM's of geese nesting at Gleddie Lake and that of those nesting at Kininvie Flat were greater than the values of other areas (Duncan multiple range test). Eggs from geese nesting at Gleddie Lake and at Kininvie Flat were also larger than those at other areas (Duncan multiple range test).

Repeatability values of egg characteristics

Defined as the among-females component of variance over the total phenotypic variance, repeatability can be used to suggest if some of the variation in a trait reflects genetic variation among individuals. I calculated the repeatability in two different ways: first using mean values from first clutches produced in two consecutive years in captivity (Table II-11) and second using

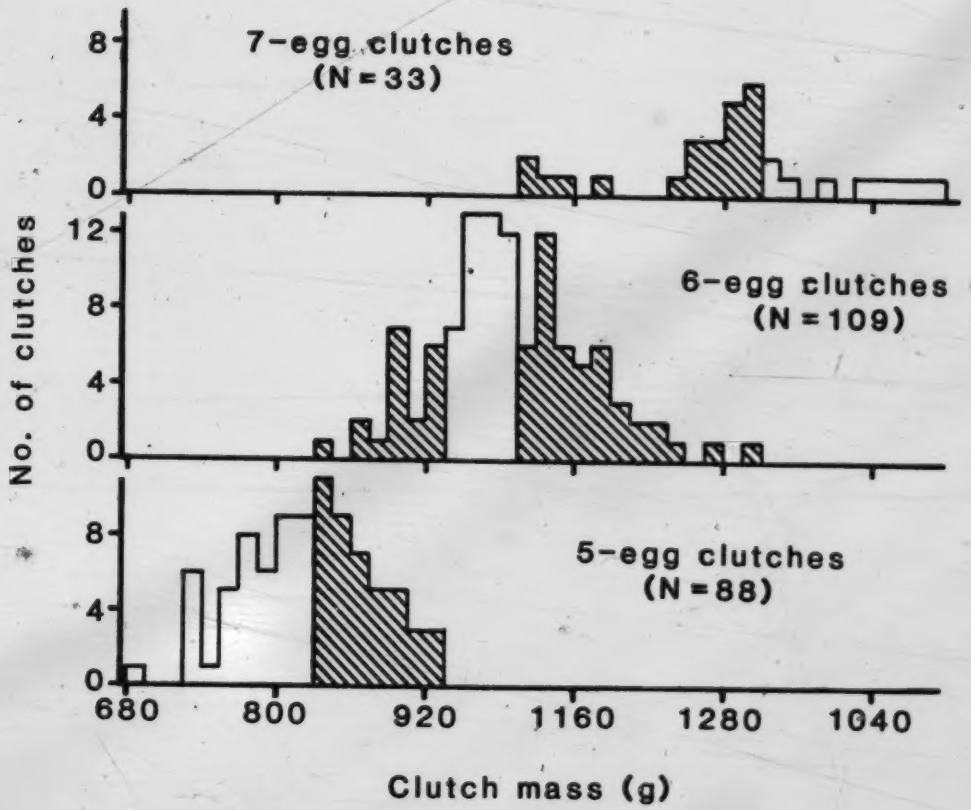

Figure II-9: Overlap in masses of five-, six-, and seven-egg clutches of wild Canada geese nesting near Brooks, Alberta. Cross-hatched areas denote overlap among clutch sizes.

TABLE II-10: Mean (±SD) of mean values of egg characteristics per clutch of 19 females producing clutches in captivity in 2 consecutive years at Brooks, Alberta. Only first clutches considered.

Characteristics	Year		Difference
	1983	1984	t[1]
Mean egg mass	161.9±10.3	163.1±10.3	1.21
Mean egg length	84.7±3.4	84.5±2.8	0.32
Mean egg breadth	58.3±1.1	58.2±1.3	0.71
Mean index of egg volume	288.0±18.5	286.5±18.1	0.32

[1] Based on a paired t-test; for all characteristics $P > 0.20$

TABLE II-11: Analysis of phenotypic variation in the egg characteristics of first clutches produced by 19 marked female Canada geese in captivity over 2 years.

Characteristics	Among female variance	Within female variance	Repeatability
Egg mass	97.394	9.103	0.915
Egg length	8.692	1.138	0.884
Egg breadth	1.297	0.190	0.872
Index of egg volume	299.232	33.858	0.898

mean values of the first clutch and the second clutch laid the same year by a given female (Table II-12). Average repeatabilities of MEM and MIV were 0.888 (±0.049) and 0.827 (±0.154) respectively. Mean breadth of eggs had the lowest repeatability ($\bar{X}$ = 0.565, SD = 0.268).

DISCUSSION

Indices of variation

Range and coefficient of variation have both been used to describe the amount of variation in egg characteristics existing in other populations of waterfowl species. The range in mass of eggs produced by Canada geese breeding in the wild near Brooks, Alberta, for the 2 years was 129-200 g (N = 1416) and the range in volume index was 227.2-374.2 cm^3 (N = 1701). The percentage the lightest was of the heaviest obtained in this study (64.5) was less than that (68) recorded by Manning (1978) from arctic nesting Canada geese (*B. c. interior*) or calculated (79) from the data of Young (1972) for greylag geese, but greater than the value (56) reported by Cooper (1978) for giant Canada geese (*B. c. maxima*) in Marshy Point, Manitoba. It was similar to values reported by Lack (1968) for emperor penguins and Ankney and Bisset (1976) for snow geese. Lack claimed that the large variation observed in his study was unparalleled in other species of birds, whereas Ankney and Bisset (1976) stated that such large variation in egg masses was unusual among species of waterfowl. The data from this study suggest that such variation may not be so unique.

However, it is important to remember that range is known to be greatly affected by outlier values and by sample size (Sokal and Rohlf 1981). Sample sizes in the study of Ankney and Bisset (1976) and this study were relatively large (N >1000) whereas those of Young (1972) involved only 200 eggs and Manning (1978) 125 eggs. Hence small sample size may have influenced their results. I tested the relationship between range and sample size by taking random samples of different sizes from data recorded in 1984.

TABLE II-12: Analysis of phenotypic variation in the egg characteristics of first clutches produced by Canada geese in captivity within a given year.

Characteristics	Among female variance	Within female variance	Repeatability
1983[1]			
Egg mass	46.864	9.550	0.831
Egg length	3.621	1.141	0.761
Egg breadth	3.298	4.121	0.445
Index of egg volume	11.276	6.082	0.650
1984[2]			
Egg mass	60.974	5.425	0.918
Egg length	5.042	0.523	0.906
Egg breadth	1.417	2.327	0.379
Index of egg volume	2.001	0.147	0.932

[1] No. of females = 13
[2] No. of females = 8

As predicted, the ratio of the lightest to the heaviest showed a clear inverse relationship with sample size (Fig. II-10). From these results, it is evident that the range is an inappropriate indicator of the variation in egg size existing in a population because it is too dependent upon the sample size.

On the other hand, the coefficient of variation may be more appropriate to describe the variation present. It can be used to test if a character is more variable in one population than in another (Sokal and Braumann 1980). The CV's for MIV in eggs produced by Canada geese in the wild in 1983 and 1984 (Table II-2) did not differ significantly from those reported by Manning (1978) for eggs of *B. c. maxima* and *B. c. interior*. The CV's of mass for eggs produced by *B. c. moffiti* near Brooks in both years (1983; 7.43, 1984; 7.26) were not different from those reported for *B. c. interior* by Manning (1978), but were different from those of *B. c. maxima*. Cooper (1978) found a larger CV in egg mass in the latter subspecies (data from 1983 compared to his data of 1970: $t = 4.363$, $df = 771$, $P < 0.001$; his data of 1971: $t = 4.558$, $df = 798$, $P < 0.001$). The CV of egg mass in a population of snow geese (Ankney 1980) was smaller than in my study (compared with 1984 data: $t = 8.63$, $df = 4951$, $P < 0.001$). In contrast, the CV of MEM of Canada geese in this study did not differ significantly from those of either a population of mallards (*Anas platyrhynchos*) or tufted duck (*Aythya fuligula*) (Hill 1984). The CV of index of volume was not significantly different from that recorded for a population of common eiders (*Somateria mollissima*; Schmutz 1981).

Ankney and Bisset (1976) suggested that the oscillation of selective pressures maintains a wide range of egg mass genotypes in the population. Based on this hypothesis, they predicted that the degree of egg mass variation (CV) would be proportional to the amount of annual variation in the environmental conditions during hatching. This prediction is very difficult to test because we do not know what particular environmental condition(s) is(are) critical to the survival of the gosling. For example, it may be a combination of rain and sub-zero temperatures or snow and strong winds that is critical.

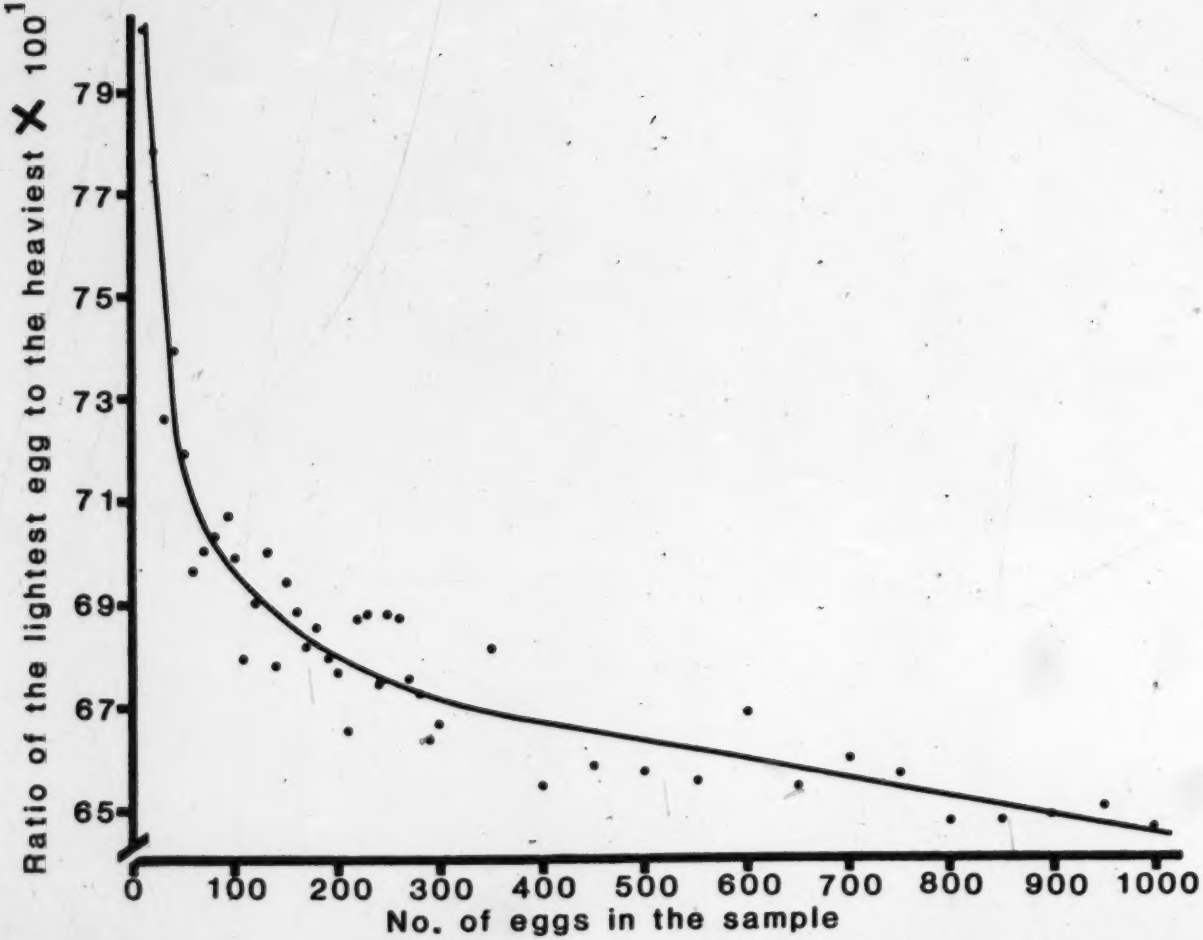

Figure II-10: Computer simulation showing the variation of the ratio of the lightest egg to the heaviest calculated in various random samples of eggs of Canada geese. Each datum represents the mean value of the ratio for five runs with a given sample size.

However, if we assume that environmental conditions during hatching at mid latitude do not vary as much as those at high latitude, the variation in egg size (CV) should be smaller in my population and that of Cooper (1978) than that of Ankney and Bisset (1976). However, we observed more variation in egg size in my study and that of Cooper (1978) than that of Ankney and Bisset (1976). To explain these results, I propose that the amount of variation in egg size may be inversely proportional to the severity of the environmental conditions and not to the amount of annual variation in the environmental conditions. Assuming that small eggs do not produce goslings of as good "quality" as large eggs, an increase in the severity of conditions would increase the selective pressures against females that lay smaller eggs, therefore reducing the variation in egg size. If these severe conditions were to persist for a long period of time (e.g. 15 generations), mean egg size would be negatively correlated with the coefficient of variation. More studies are needed to document the amount of variation of egg size within a species along a gradient of severity in environmental conditions to see if there is any relationship between these two variables.

Variation in egg characteristics within clutches in Canada geese

The magnitude of the variation among eggs within clutches, obtained from geese in captivity and in the wild, was lower for all characteristics than that reported by Manning (1978). Because this is a relative measurement of the variation, the difference between these two sets of results could reflect a larger variation among clutches or a smaller variation within clutches. Vaisanen et al. (1972) reported that 19.5 to 40.5% of the total variance in egg volume could be explained by variation among eggs within clutches for five species of waders. In some passerines, this value varied from 19 to 27.6% (Ojanen et al. 1979, Jarvinen and Vaisanen 1983). Differences between species may depend on factors such as the presence of asynchronous hatching or the different means of resource acquisition of the laying female (endogenous versus exogenous sources).

The variation in egg characteristics within clutches was related to the laying sequence (Figures II-5 to II-9, Tables II-4 and II-5). Cargill (1979) also found significant associations between egg mass and laying sequence in snow geese; the last egg was on average significantly lighter than earlier eggs for three-, four-, and five-egg clutches. Cooper (1978) reported a similar curvilinear pattern for egg mass in Canada geese. However he did not consider the possible existence of this relationship within each clutch size. In the wild, the second egg appeared to be the heaviest in 4-egg clutches, however for 5-egg, 6-egg, and 7-egg clutches, it was either the second, the third, or the fourth without any clear dominance of one position (Table II-13). Therefore the differences in egg size within a clutch are mainly between the first and last eggs, and those in the middle of the clutch. In a sample of 120 clutches, the lightest egg was the first egg in 44% of the clutches and the last egg in 45%. Furthermore, no significant difference were found between the mass of the first and last egg. These results contrast with those of Raveling and Lumsden (1977) and Wang (1982) who found that the last-laid egg was the smallest of the clutch.

By comparing the last egg only to the eggs earlier in the sequence (see Manning 1978), the pattern of variation within clutches may be incorrect because the information about the first egg is masked or diluted (it represents only one-third to one-sixth of all earlier laid eggs). Data should not be pooled, otherwise the within clutch size variation will be masked.

Koskimies (1957) found significant effect of laying sequence on egg breadth in 12 clutches. The pattern of variation in his study of egg breadth was very similar to that in this study. If breadth is as closely correlated with egg mass as in this study ($r^2 = 0.689$, $df = 120$, $P < 0.001$), then the eggs of the white-winged scoter (*Melanitta fusca*) will follow a similar pattern of variation within a clutch.

Intraclutch variation in egg size has been documented also in gulls (e.g., Parsons 1970, 1976, Lundberg and Vaisanen 1979, Mills 1979, Furness 1983, Houston et al 1983), in passerines (see Ojanen et al. 1981 for a review), in

TABLE II-13: Frequency with which the heaviest egg occurred in each position in the laying sequence within a given clutch size. Clutches of wild and captive Canada geese were combined.

Clutch size (N)[1]	Position in the laying sequence							G^2	P[3]
	1	2	3	4	5	6	7		
4 (21)	3	13	3	2	---	---	---	13.00	< 0.005
5 (62)	7	20	25	7	3	---	---	29.66	< 0.001
6 (74)	7	19	19	20	9	0	---	38.59	< 0.001
7 (22)	2	8	8	3	1	0	0	25.52	< 0.001

[1] No. of clutches
[2] G statistic of the log-likelihood test goodness of fit
[3] Probability that the null hypothesis (i. e. the heaviest egg is equally likely to occur in any position in the laying sequence) is true

raptors (Edwards and Collopy 1983), and in shorebirds (e.g., Miller 1979, Nol et al. 1984).

Three hypotheses have been proposed to explain the adaptive value of such variation in egg size within clutches. For species in which the size of eggs decreases with laying sequence, such variation is thought to facilitate the brood reduction in the face of food scarcity by adding differences in mass and size to differences in age between members of the same brood (Parsons 1972, O'Connor 1978, 1979, Lundberg and Vaisanen 1979, Slagsvold et al. 1984). For species in which the size increases with laying sequence, such variation is seen as a countermeasure preventing the potentially adverse effects of being hatched last in an asynchronous hatch by equipping the last hatchling with more food reserves and thus, prolonging its survival (Howe 1976, Rydén 1978, Horsfall 1984). However, Clark and Wilson (1981) suggested that asynchronous hatching was an adaptation to reduce the time spent by the egg or the chick in the nest between laying and fledging, thus reducing the probability of being preyed upon. If in this case, chicks were all of the same size at hatching, last hatched chicks would be at a size disadvantage only as a consequence of asynchronous hatching. To offset this cost of asynchrony, late-hatching eggs should be larger (Clark and Wilson 1981).

Non-adaptive hypotheses to explain egg size variation within clutches have also been proposed. Parsons (1976) suggested that physiological changes caused by hormonal changes occurring at the onset of incubation could explain the variation in egg size within a normal clutch in herring gull (*Larus argentatus*). However it is unknown how these changes produce the observed variation in egg size within a clutch. The lipid reserves of the laying female lesser black-backed gull (*Larus fuscus*) may influence the size of the last egg. Gochfeld (1977) also suggested that in the common tern (*Sterna hirundo*), the ability of the female to obtain adequate food during laying might affect the size of the last egg (Houston et al. 1983).

In Canada geese, these hypotheses concerning the adaptive value of within clutch variation in egg size are rejected as possible explanations of

such variation because they can only explain consistent decreases or increases throughout the laying sequence, neither of which occurred in this species. Furthermore, the brood reduction strategy is an unlikely explanation in this case because parents do not feed their goslings. Consequently, the number of offspring the parents can raise is independent of their capacity to bring food. Because the last egg hatches last in most cases (Cargill and Cooke 1981, but see Cooper and Hickin 1972) and is one of the smallest eggs, Clark and Wilson's (1981) hypothesis can also be rejected.

In Canada geese, the risk of predation on uncompleted clutches probably decreases consistently from the first to the last egg laid because females become progressively more attentive during laying (Cooper 1978). To reduce the potential loss of reproductive effort to predation, egg size should increase with the laying sequence. However because hatching order is correlated with laying order, egg size should decrease with laying sequence to reduce the cost for the adult female of leaving unhatched or unprepared goslings in the nest because of an unexpected early brood departure. On this point, Cargill (1979) found that last eggs were more likely to be abandoned in the nest than earlier eggs in the sequence. From this, one would predict a curvilinear relationship in egg mass with laying sequence. A female would invest less in the first few eggs because their higher risk of predation and similarly she would invest less in the last few eggs because their higher probability of being left in the nest. In addition, a curvilinear pattern of egg mass may produce a social hierarchy within the brood, which could be reflected in different risks of predation on the egg or/and chick as in the American oystercatcher (*Haematopus palliatus*; Nol et al. 1984).

Although this model may explain the variation of egg size within a clutch, I suggest that proximal causes are a more likely explanation of this pattern. The first egg may be smaller because parts of the reproductive tract such as the oviduct and its associated glands, have not reached their full capacity. Once this is attained, eggs would be very similar in size as those in the middle of most clutches of Canada geese. However, just prior to the

formation of the 2 last eggs, a stimulus may affect the onset of incubation and indirectly reduce egg size. Parsons (1976) and Astheimer and Grau (1985) suggested that the smaller size of the last egg was caused by a reduction of the albumen content. The stimulus could cause a decrease in albumen synthesis which would result in the addition of less water in last egg(s) (Astheimer and Grau 1985). The decrease in egg size for the two last eggs could also be due to a reduced quantity of materials available for the formation of the last eggs (Romanoff and Romanoff 1949). However, it seemed unlikely because it required the same time for captive geese to lay the last egg as to lay the second egg in a clutch (paired t-test: $t = 0.287$, $DF = 73$, $P = 0.70$). Protein reserves are known to decrease between the start and the completion of laying (Jones and Ward 1976, Ankney and MacInnes 1978, Pinowska 1979, Bromley 1984). A reduction in the concentration of calcium in the diet resulted in lighter egg in domestic fowl (Gilbert 1983). However, the quantity of calcium present in the medullary bone of Canada geese seemed sufficient for egg production because the content of calcium in the femur and tibiotarsus was greater at the end of egg laying than during the non-reproductive season (Raveling et al. 1978). More studies using stains or radioactive marking techniques on nutrients incorporated into eggs (e.g., Astheimer and Grau 1985) could answer some of these questions about egg size and laying sequence.

Variation in egg characteristics among females

In the eggs of Canada geese produced in the wild, the variance among clutches actually represents a combination of two sets of variances: the variance resulting from differences among females and the variance resulting from differences among clutches of a given female. Because no attempts were made to identify continuation clutches (Cooper 1978), renests, and nests of a given female in 1983 and 1984, I could not estimate the latter source of variance. However data from the captive flock for which such an estimate was available, suggest that its contribution to the total variance is very small

(Table II-3). Therefore, it appears that the variation among clutches in the wild is a good estimate of the variation in egg characteristics among females.

Among the variables considered as potentially contributing to this variation, body condition of the female seemed to be the only one that could explain some (17%) of the variation of egg size among females. Because the body condition of females decreases from laying to the end of incubation (Ankney and MacInnes 1978, Aldrich and Raveling 1983, Mainguy and Thomas 1985), the coefficients of correlation between body condition and mean egg mass would perhaps have been greater had the index of condition been calculated from pre-laying mass. In view of the many similarities between the results from captive and wild geese, body condition would be the only important environmental factor affecting the extent of variation in egg size in the wild. Jarvinen and Vaisanen (1983, 1984) showed that the mass rather than the size of the female (determined by the length of the wing) influenced egg size variation in the pied flycatcher (*Ficedula hypoleuca*). Although they did not have data to support this, they associated mass of the female with "fatness". Also, mean egg mass was correlated with female mass but not with tail, wing, tarsus, or bill length in the house sparrow (*Passer domesticus*; Murphy 1977). These results are in contrast with those of Otto (1979) who found that large females (determined again by the length of the wing) but not heavy females, laid large eggs in fieldfare (*Turdus pilaris*).

Diet quality before laying and during laying affects egg masses in mallard (Krapu 1979), ruffed grouse (*Bonasa umbellus*; Beckerton and Middleton 1982), and in magpies (*Pica pica*; Hogstedt 1981). In this last species supplemented food has been shown to affect egg mass (Hochachka 1985). But in none of these studies is it known how diet was manifested in prelaying mass and body condition of the female. In the common tern, the quantity of food brought to the female during laying was correlated with the mean egg size (Nisbet 1973). Protein reserves rather than fat reserves seemed to be important in determining egg size in lesser black-backed gulls (Houston et al. 1983).

Arctic nesting geese accumulate large fat reserves before laying (Ankney and MacInnes 1978, Raveling 1979, Gauthier et al. 1984). During this period, body mass partly reflects body condition of the bird and therefore becomes inappropriate as an index of body size. In my study, I circumvented this problem by using an index of body size derived from a principal components analysis of morphometric measurements. In interspecific comparisons among the members of the Anseriformes, Lack (1968) and Owen (1980) found that proportionate egg size (mean egg mass / body mass) increased with body size, (using body mass as an index of size). However, Ankney and Bisset (1976) and Batt and Prince (1978) found no relationship between body mass and egg size in either snow geese or mallards. I also found no relationship between these parameters in the captive flock of Canada geese. These results contrast with studies of shorebirds (e.g., Vaisanen et al., 1972, Nol et al. 1984), passerines (e.g., Murphy 1978, Grant 1982), gulls (e.g., Mills 1979), and grouse (Myrberget 1977) in which body size is positively correlated with egg size. However in some of these studies, body mass was used as an index of body size and consequently they must be interpreted with care. Body size and egg size are known to be controlled by independent genes and pleiotropic genes in the domestic chicken, *Gallus domesticus* (Festing and Nordskog 1967). It is therefore possible that selective pressures acting on body size could affect the variation on egg size. However in this study, because these two characters were not associated to each other, I could not predict a change in egg size if body size were to change.

In many species of gulls, young females are known to lay smaller eggs than older ones (e.g., Coulson 1963, Mills 1979, Furness 1983, Thomas 1983). In Canada and Hawaiian geese (*B. c. sandvicensis*), Copper (1978) and Kear and Berger (1980) also reported an increase in mean egg mass up to a certain age, depending upon the species. Past that age, it has been shown to decrease. Owen (1980) found that the eggs of captive barnacle geese (*B. leucopsis*) breeding for the first time weighed 2% less than those of older birds. However, no evidence of an age effect was found in giant Canada

geese (Wang 1982), captive mallards (Batt and Prince 1979) and common eiders (Baillie and Milne 1982). In my study, except for two females that were 4 years old, all females were 5 years old or older. This was probably the reason that I did not detect any effect of age. However, even if age is important, it is very difficult to separate the effect of condition or experience from that of age.

If there is a trade-off between the size and the number of offspring produced (Smith and Fretwell 1974), we should expect a negative correlation between mean egg size and clutch size. My data in captivity and in the wild do not support this hypothesis. In fact there was so much variation in mean egg mass within a given clutch size that a considerable overlap existed between two adjacent clutch sizes in total mass of the clutch (Fig. II-10). The extent of overlap was very similar to that reported by Ankney and Bisset (1976). These authors and Cargill (1979) did not find any relationship between egg size and clutch size. No significant relationship between clutch size and egg size was found by either Koskimies (1957) in the white-winged scoter, or by Hill (1984) in mallards and tufted ducks. Batt and Prince (1979) reported a significant positive but weak relationship between egg size and clutch size for first nests and all renesting attempts in a captive population of mallards. In their study, females in good condition probably laid larger clutches and larger eggs than females in poorer condition. Manning (1978) reported a negative correlation between egg characteristics and clutch size in some areas. However when pooled, his data did not show any significant trend with clutch size except for length. Thus, there is very little evidence that egg size variation is the result of a trade-off between the number and the size of offspring.

A significant decrease of egg size of Canada geese with date of laying was evident among wild birds in one area in 1984. Cooper (1978) also reported a significant decrease in egg mass with date of nest initiation, but the proportion of the variance explained by date of laying was only 2.2 to 2.6%. In mallards, Batt and Prince (1979) found an increase in MEM from the

first to the third clutch in a given season but in the fourth, the MEM decreased to the level of the first clutch. Koskimies (1957) also found an increasing trend of egg size of white-winged scoters with date of laying but it was not statistically significant. Hill (1984) found a significant decrease of MIV with date of laying in the tufted duck but not in the mallard. In geese, young females tend to lay later (Brackage 1965, Finney and Cooke 1978) and smaller eggs (Cooper 1978, Kear and Berger 1980) which could explain why mean egg size decreased with date of laying (Cooper 1978). However, no differences were found in mean egg mass between two successive clutches within the same year in captivity (paired t-test; 1983: $t = 1.83$, $df = 12$, $P = 0.093$, 1984: $t = 1.10$, $df = 7$, $P = 0.306$). Therefore date of laying appears to have a little or no influence on egg size variation among females unless it is reflected in food availability, a factor kept constant in captivity.

Repeatability of MEM and MIV in the eggs of captive Canada geese

The repeatability of MEM and MIV of eggs obtained from captive geese appears to be higher (Table II-11) than values reported previously in the literature. For MEM or MIV, values were 0.62 in mallards in captivity (Batt and Prince 1978), 0.73 to 0.77 in red grouse (*Lagopus lagopus scoticus*; Moss and Watson 1982), 0.29 to 0.52 in oystercatcher (Nol et al. 1984), 0.62 to 0.72 in two species of Darwin's finches (*Geospiza magnirostria, G. conirostris*; Grant 1982), and from 0.09 to 0.80 in great tits (*Parus major*; van Noordwijk et al. 1981). Deriving the repeatability values from a hierarchical ANOVA (repeatability = the among-females component of variance over the total variance), Vaisanen et al. (1972) obtained values ranging from 0.538 to 0.810 in five species of waders, whereas Ojanen et al. (1979) reported values of 0.440 to 0.766 in four species of passerines.

Repeatability sets an upper limit to the estimation of heritability of a trait (Falconer 1960). However because spatial changes in the environment were very limited in most of the above studies, the estimates of repeatability indicated mainly the importance of temporal changes in the environment (van

Noordwijk et al. 1981). In the wild, if females use the same territory year after year, differences in egg size could result from consistent differences in the way environmental factors affect each female. In captivity, this problem is greater than in the wild because in most cases the environment is even more similar between repeated measurements of the trait. However, despite these problems, repeatability and heritability estimates were found to be very similar in mallards (Prince et al. 1970, Batt and Prince 1978), in great tits (van Noordwijk et al. 1981), and in red grouse (Moss and Watson 1982). Based on this argument, my data support the hypothesis that a major part of the differences in mean egg size between females reflects genetic differences. However, it is a poor test because repeatability and heritability should be estimated in the wild using marked birds. However, the similarity in the percentage of the total variance explained by within and among females for captive and wild geese suggested strongly that environmental conditions had little effect on egg size unless the wild conditions were extremely similar to the captive. I do not believe that it was the case.

Variation in egg characteristics of Canada geese among years

Differences in MIV of eggs produced in different years were not detected in any of the populations studied in the wild at Brooks, Alberta, apart from a significant increase at Gleddie Lake in 1984. Cooper (978) recorded significant annual variation in MEM in Canada geese and Milne (1974) in common eiders. Studies of some non-anseriform species also showed yearly changes in MEM or MIV (e.g., Jenkins et al. 1967, Vaisanen et al. 1972, O'Connor 1979, Jarvinen and Vaisanen 1984, Moss et al. 1984).

Increase of MEM but not MIV in 1984 at Gleddie Lake resulted in a higher mean egg density in 1984 ($t = 6.22$, $df = 73$, $P < 0.001$). Changes in density could not be tested in other areas because only small sample sizes of clutches with known MEM and MIV were available. However I tested for changes in density of eggs from captive birds and found that, as at Gleddie Lake, eggs had a higher density in 1984 compared to 1983 ($t = 5.108$, df

= 53, $P < 0.001$). An analysis of covariance using the data from Gleddie Lake and in captivity showed that for any given MIV, MEM was higher in 1984 (Gleddie Lake: $F = 41.37$, $df = 1,73$, $P < 0.001$; captivity: $F = 26.490$, $df = 1,52$, $P < 0.001$).

Because egg size might be related to the age of the female, specially with young females, a change in the age structure of the population could change the mean MEM in one area. However not all eggs would be heavier as was the case. And besides, a change in the proportion of young females nesting would not have affected the relationship between MEM and MIV as it did for geese nesting at Gleddie Lake and in captivity. Food availability could not explain the change in MEM because in captivity there were no difference between years in the amount of food provided to the females during nesting. A change in food availability was a possible cause of the change in egg density of the shag (*Phalacrocorax aristotelis*) over 2 years of study (Snow 1960). Geese at Gleddie Lake in 1984 nested later than in 1983 (Mann-Whitney $U = 710$, $N_1 = 45$, $N_2 = 44$, $P = 0.02$). However no differences were found in captivity (Mann-Whitney $U = 289.5$, $N_1 = 34$, $N_2 = 21$, $P = 0.24$). Therefore, it does not appear that the timing of laying is a contributing factor to the difference between years of MEM or the density.

Positive correlations between ambient temperature and egg volume were reported in starlings (*Sturnus vulgaris*) and pied flycatchers (Ojanen et al. 1981). Howe (1976) reported a curvilinear relationship between adjusted fresh egg mass and temperature minima in the common grackle (*Quiscalus quiscula*). Because the captive flock is located approximately 30 km from Gleddie Lake, the temperature regime was probably very similar in both places. Therefore any differences between years in the temperature regime may have affected the formation of eggs. However, no conclusive statement can be made with only 2 years of study.

Variation in egg characteristics of Canada geese among areas

Egg size is known to vary between distant study areas (e.g., Vaisanen 1969, Anderson et al. 1970, Batt and Prince 1978, Murphy 1978, Miller 1979). These major geographic differences appeared to be related to differences in body size of the females from nearby areas (Anderson et al. 1970, Vaisanen 1977, Miller 1979). Such differences in body size of the females are unlikely to explain differences in MEM and MIV in nearby areas. Murton and Westwood (1974) found heavier eggs on arable farmland than on natural grassland in the lapwing (*Vanellus vanellus*), perhaps because of the food quality. Otto (1979) found that colonies of fieldfare with a larger biomass of lumbricids available as food had larger MEM than other colonies. Manning (1978) and Jarvinen and Vaisanen (1983) did not find differences between nearby study areas in egg size of Canada geese and of the pied flycatcher.

Difference in the age structure of the breeding population could have led to this difference in MEM and MIV noted in this study. Areas with smaller MEM or MIV could have had proportionally more young females laying completed clutches. Unfortunately this could not be tested because the ages of the females in the wild were unknown. Coulson (1963) used egg masses to estimate the age structure of populations of black-legged kittiwake (*Rissa tridactyla*). It assumes that the body condition of the females was not different among areas. I was unable to test this hypothesis because no indices of condition were determined from wild breeding birds.

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III. REPRODUCTIVE SUCCESS OF CANADA GEESE: INFLUENCE OF EGG SIZE, POSITION IN THE LAYING SEQUENCE, AND BROOD SIZE

INTRODUCTION

Reproductive success can be estimated at different stages of the life history of a species. The number of eggs hatching and the number of chicks fledging represent valid estimates of reproductive success in birds (Howard 1979).

Extrinsic (environmental) factors such as predation (e.g., Vermeer 1970, Cooper 1978), climatic conditions (e.g., Cooper 1978), intraspecific competition (Ewaschuk and Boag 1972), and food availability on staging areas (e.g., Ankney and MacInnes 1978, Gauthier et al. 1984) can affect hatching and fledging success in Anserinae. Intrinsic factors such as egg size, egg quality, and position in the laying sequence have been studied in nidicolous species and found to influence hatching and fledging success (e.g., Parsons 1970, Murton et al. 1974, Howe 1976, O'Connor 1978, Rofstad and Sandvik 1985). By contrast, this aspect of the life history of nidifugous species has received little attention in a natural environment apart from the work of Cooper (1978) and Wang (1982). The proportion of chicks reaching fledging age increases with increasing initial brood size in some nidifugous species (e.g., Heusmann 1972, Glasgow 1977, Clawson et al. 1979, Rohwer 1984) but not in others (e.g., Safriel 1975, Andersson and Eriksson 1982).

In this paper, I examined the effects of egg size and position in the laying sequence on hatching and fledging success of wild Canada geese (*Branta canadensis*). In addition, I reported on the relationship between fledging success and brood size at hatching.

STUDY AREA AND METHODS

This study was carried out in 1983 and 1984 near Brooks (50° 35' N, 111° 54' W), in the shortgrass ecoregion of southeastern Alberta (Strong and Leggat 1981). The field work was conducted from late March to early July

each year.

Hatching success is defined here as the percentage or proportion of eggs surviving to the time of hatching that produced a chick (see Koenig 1982). The data on hatching success came from two sources: nests at Gleddie Lake (Fig. II-1) which were monitored from laying to hatching and, nests from other lakes (Fig. II-1) which were also monitored from laying to hatching but were artificially incubated during the last week of incubation (see Chapter IV). I searched Gleddie Lake daily in 1983 and every 2 days in 1984. Other areas were checked every 2 to 4 days.

Upon discovery of a nest, I marked each egg with a waterproof felt pen with the date of discovery. I also determined the sequence of laying by the degree of whiteness of eggs (Cooper 1978) in nests with less than four eggs. Subsequent visits during laying allowed me to determine the laying sequence of the rest of the clutch. The mass, breadth at largest diameter, and maximum length of each egg were recorded. Fresh mass of already incubated eggs was estimated using average loss of mass during incubation (Fig. II-2) or by using a known relationship between the fresh mass of an egg and its index of volume (Fig. II-3).

The fate of each clutch was classified as successful, predator destroyed, flooded, deserted, or incubated but not hatched. A clutch was considered successful if at least one egg hatched. In each successful clutch, the fate of each egg was classified as successful, disappeared, preyed upon, broken, incubated but not hatched, or flooded. An egg was considered successful if a gosling emerged from the shell. No attempt was made to determine the reason why fully-incubated eggs did not hatch (whether they were infertile or suffered embryonic death). Field determination of fertility (Kossack 1950) appears to be unreliable (Cooper 1978).

All goslings hatched artificially were weighed to the nearest 0.1 g on a Sartorius scale (160 g capacity) within 4 hours of emergence from the shell. Culmen and tarsus length were determined for 36 goslings hatched from artificially incubated eggs (one per clutch). I was also able to determine the

mass, tarsal length, and culmen length of one to three goslings per clutch in several nests (N = 22) from wild geese.

Brood size was defined as the number of goslings that left the nest bowl. Individual members of many broods were marked at the time the eggs were pipped, each embryo being marked in the egg with a numbered web-tag (after Alliston 1975). I marked 171 goslings from 32 broods in 1983 and 151 from 30 in 1984. Subsequently banding drives were conducted to capture flightless adults and goslings at Gleddie Lake and at an adjacent slough (located 1 km west of Gleddie Lake). The banding drives were done 8 and 6 weeks after the peak of hatching in 1983 and 1984 respectively. For each individual captured, I determined its sex, length of tarsus, culmen, and wing chord, and mass to the nearest 25 g with a Pesola scale (5000 g capacity). All goslings were examined for the presence of a web-tag. Because most of the mortality of goslings occurs during the first 2 weeks of life (e.g., MacInnes et al. 1974, Zicus 1981), I considered the number of goslings recaptured as a estimate of the number reaching fledging age. Goslings of this subspecies (*moffiti*) are reported to attain flight at ages ranging from 7 to 8 weeks (Bellrose 1980).

RESULTS

Hatching success

The effects of egg size and position in the laying sequence on hatching success are poorly known in nidifugous species. The survival of eggs through the incubation period can be affected by predation, accidental breakage, and abandonment. Hatching success can be reduced by infertility and reduced hatchability.

In seven nests in which at least one egg was found broken without any apparent reasons such as strife between adjacent territorial pairs or predation, these eggs were not different in mass than the intact eggs of their clutch (Wilcoxon signed ranks test; $T = 0.507$, $P > 0.30$). The low

frequency of such events precluded any meaningful analysis in relation to position in the laying sequence.

To test the effect of egg size or position in the laying sequence on infertility and/or embryonic death, I used only data from successful nests. This procedure reduces the potential combination of parental effects and the two factors studied. In nests in which at least one fully-incubated egg did not hatch, the mean mass of these unhatched eggs was not different from the mean mass of successful eggs within the same clutch (Wilcoxon signed ranks test; $T = 0.90$, $P > 0.35$, no. of clutches = 33). To study the effect of position, data collected in 1983 and 1984 at Gleddie Lake and from clutches artificially incubated (only during the last week of embryonic development) were pooled to increase cell frequencies since there were no differences between naturally and artificially incubated clutches in the proportion of unsuccessful eggs (G-test; $G = 0.961$, $df = 2$, $P > 0.50$). The analysis indicated that the frequency of failure of eggs to hatch did not differ among positions in the laying sequence (Table III-1). A relatively constant proportion (7.2%) of fully incubated eggs failed to produce a gosling. To summarize, neither egg size nor position in the laying sequence affected significantly hatching success.

Fledging success

The effect of egg size on fledging success could be translated through hatching size if a relationship between egg size and hatching size existed. This was tested using one datum per clutch and a regression analysis of fresh egg mass and hatching mass of the damp gosling. Hatching mass was highly correlated with both fresh egg mass (Fig. III-1) and index of volume ($r = 0.846$, $N = 54$, $P < 0.001$). Hatching mass was also correlated with fresh egg mass within individual clutches ($\bar{X}$ of $r = 0.791$, $SD = 0.310$, $N = 29$, $P < 0.001$). Egg mass was also a good predictor of tarsus length of newly hatched goslings ($r = 0.623$, $N = 35$, $P < 0.001$) but not culmen length ($r = -0.156$, $N = 35$, $P > 0.20$). To recapitulate, larger and heavier eggs give

TABLE III-1: Number of fully incubated eggs that either successfully produced a gosling or failed to do so for a given position in the laying sequence.

	Position in the laying sequence		
	First	Middle	Last
Successful	92	346	88
Unsuccessful	6	23	9
Probability[1]		$P > 0.50$	

[1] Probability determined by a G-test, comparing numbers of successful and unsuccessful eggs

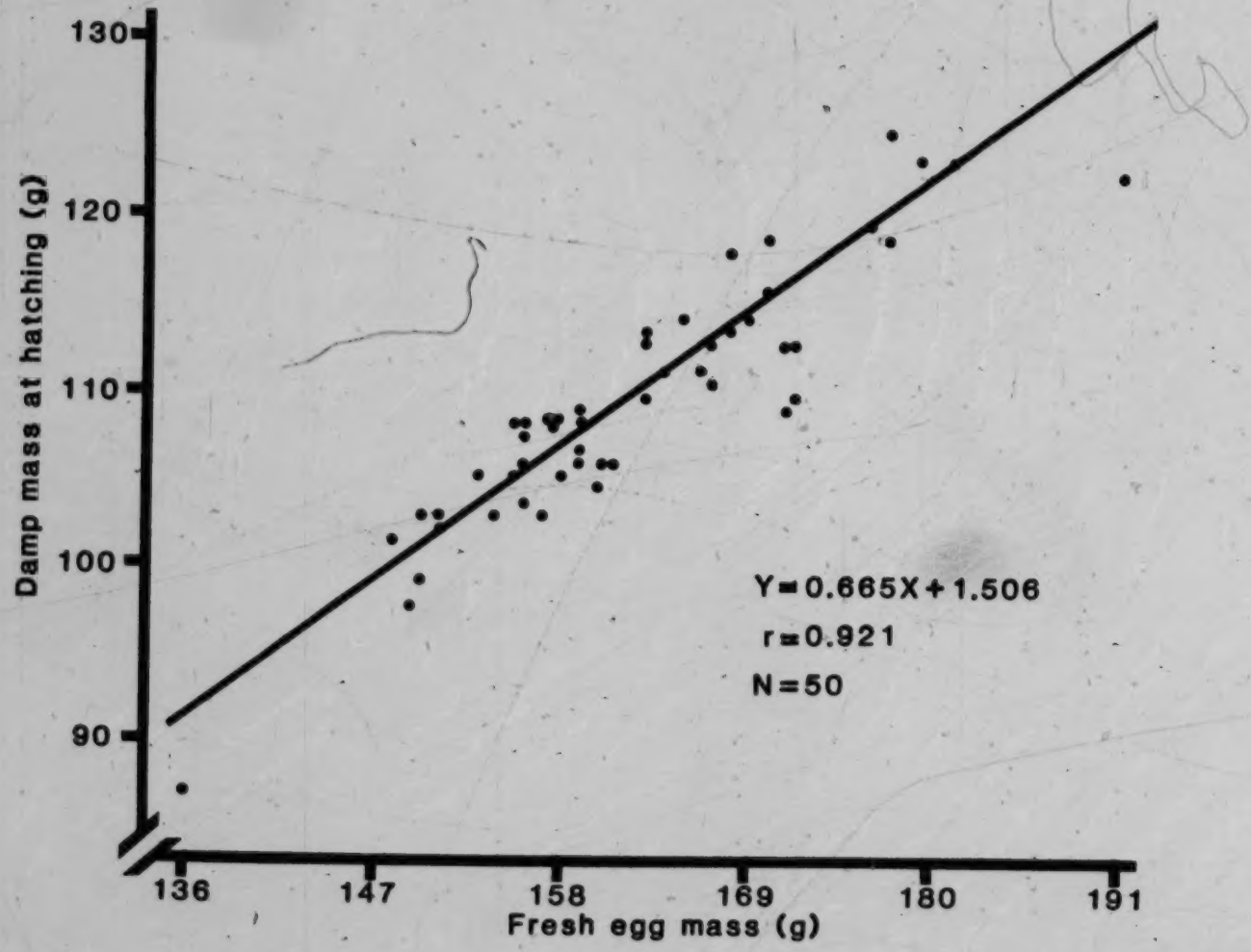

Figure III-1: Relationship between fresh egg mass (g) and mass of damp wild goslings at hatching.

rise to heavier goslings with longer tarsi.

To study the effect of egg size and position in the laying sequence on fledging success, I included only the data from broods in which I recaptured at least one gosling. Among the 40% (13/32) and 33% (10/30) broods in which no goslings were recaptured, a high percentage had probably moved overland to other areas or simply fledged and left the study area by the date of the banding drive. There were no relationships between the size of a brood and its probability of disappearing in 1983 (G-test: $G = 2.23$, $df = 2$, $P = 0.31$) and 1984 ($G = 2.79$, $df = 4$, $P = 0.41$). Overland movement is a common phenomenon in this region (Giroux 1980, pers. obs.). Thus, to assume that these broods were totally destroyed would be very unrealistic. Their departure did not invalidate my approach because the purpose of this study was not to determine an overall survival rate but to test the effect of specific factors on fledging success.

The mean egg mass of clutches in which at least one gosling was recaptured, was smaller from clutches in which no goslings were recaptured in 1983 (t-test; $t = 2.40$, $df = 30$, $P = 0.02$) but not different in 1984 ($t = 1.27$, $df = 27$, $P = 0.22$). The percentage of goslings recaptured in a clutch was not related to mean egg mass of the clutch in either 1983 or 1984 (Fig. III-2). Within each clutch, there were also no differences between the mass of eggs of recaptured and not recaptured goslings in either 1983 (Wilcoxon signed ranks test; $T = 0.283$, $P > 0.75$, no. of clutches = 19) or 1984 ($T = 0.440$, $P > 0.66$, no. of clutches = 19).

Likewise, the position in the laying sequence did not affect rates of recapture in either 1983 or 1984 (Table III-2), nor were there differences in the frequency of goslings recaptured between years for any given position (Table III-2).

The effect of brood size on survival rates was investigated by comparing brood size at hatching with the number of goslings recaptured per brood. The number of goslings recaptured per brood was not statistically different among brood sizes in 1983, 1984, and the 2 years combined (Table

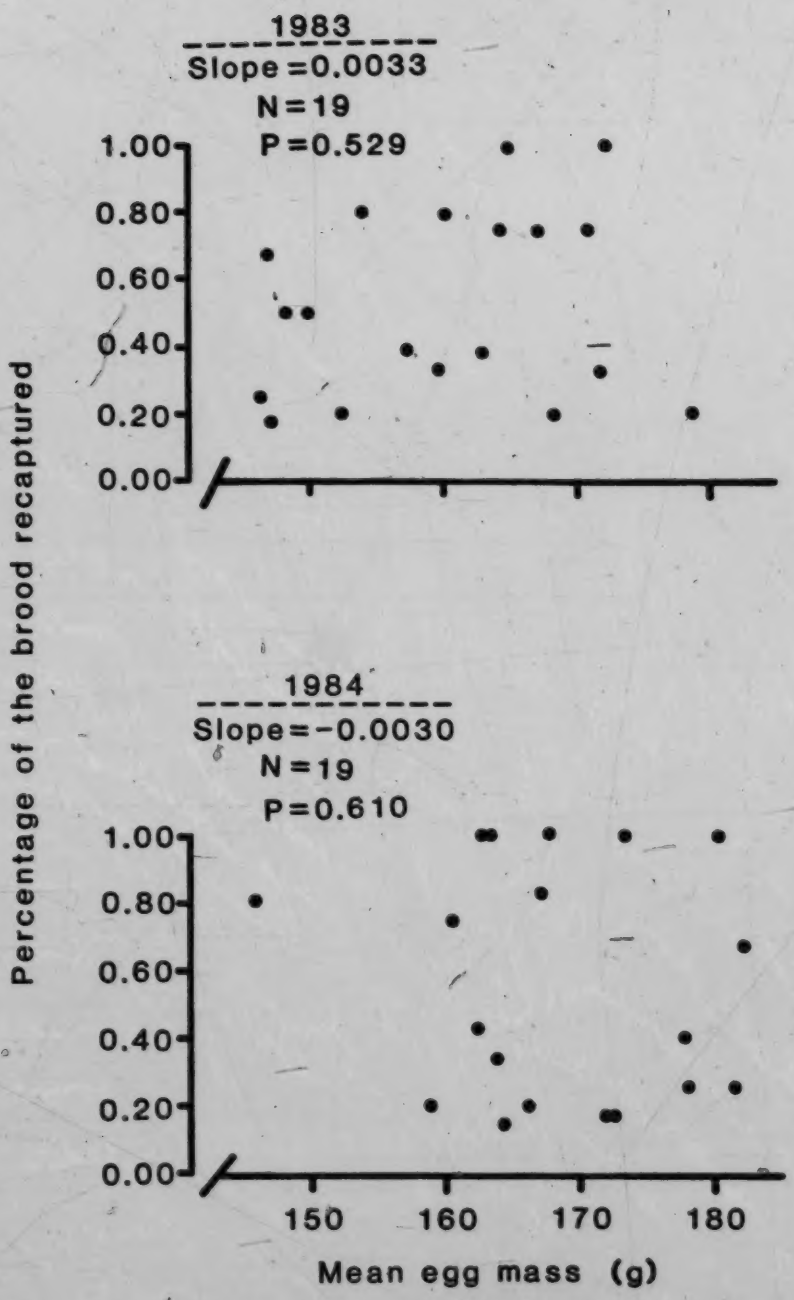

Figure III-2: Relationship between mean egg mass and percentage of goslings recaptured from broods of Canada geese, in 1983 and 1984 (slope derived from a test for a linear trend in proportion; Snedecor and Cochran 1980).

TABLE III-2: Number of goslings that were either marked and recaptured, or marked and not recaptured for a given position in the laying sequence.

	1983		1984		
	Recaptured	Not recaptured	Recaptured	Not recaptured	Probability[1]
First	6	11	11	5	0.052
Middle	35	29	31	30	0.665
Last	6	10	7	9	0.719
Probability[1]	0.226		0.316		

[1] Probability determined by a G-test, comparing numbers of goslings recaptured and not recaptured

TABLE III-3: Average number of goslings recaptured in different sizes of brood.

	1983		1984		Years combined	
Brood size[1]	$\bar{X}$±SD	N	$\bar{X}$±SD	N	$\bar{X}$±SD	N
1	1.00	1	-----	--	1.00	1
3	-----	--	3.00±0.00	2	3.00±0.00	2
4	2.50±1.00	4	2.83±1.47	6	2.70±1.25	10
5	2.57±1.72	7	2.00±1.41	4	2.36±1.57	11
6	2.40±1.14	5	2.60±1.82	5	2.50±1.43	10
7	3.00	1	2.00±1.41	2	2.33±1.15	3
8	3.00	1	-----	--	3.00	1
P[2]	0.865		0.859		0.898	

[1] Number of goslings leaving the nest bowl
[2] Probability determined by a Kruskal-Wallis oneway ANOVA, comparing numbers of goslings recaptured per brood

III-3). To see whether larger broods lost proportionately more goslings than smaller broods, I tested whether the slope of a regression line drawn through the logarithms of the number recaptured and the initial brood size, was different from one (after Ricklefs et al. 1978). I found that larger broods lost proportionately more goslings than smaller broods ($t = 2.688$, $df = 17$, $P = 0.02$) in 1984 but not in 1983 ($t = 1.772$, $df = 17$, $P = 0.09$). This was not the result of larger broods being exposed for a longer period of time to causes of mortality because there was no relationship between age of the brood and proportion of goslings recaptured in a brood (Fig. III-3).

DISCUSSION

Hatching success

Effect of egg size

Neither egg size nor position in the laying sequence influenced hatching success in Canada geese in this study which concurs with some other published studies. The size of an egg did not affect its hatching success in the following nidifugous species: snow geese (*Chen caerulescens*) (Cargill 1979), red grouse (*Lagopus lagopus scoticus*) (Moss et al. 1981), ring-billed gulls (*Larus delawarensis*) (Ryder 1975) and as well as nidicolous species: tree swallows (*Tachycineta bicolor*) (De Steven 1978), European swifts (*Apus apus*) (O'Connor 1979), or hooded crow (*Corvus corone cornix*) (Rofstad and Sandvik 1985). The last authors suggested that their data were showing a relationship between egg size and hatching success. However I disagree with their conclusions because 40% of the eggs that failed to hatch were larger than the mean egg size of all the eggs. An interspecific analysis failed to detect any relationship between mean egg size of a species and its average hatching success (Koenig 1982). By contrast, the size of eggs was related to hatching success: those failing to hatch were significantly smaller than those hatching in giant Canada geese (*B. c. maxima*) (Wang 1982), woodpigeons (*Columba palumbus*) (Murton et al. 1974), laughing gulls (*Larus atricilla*) (Schreiber et al.

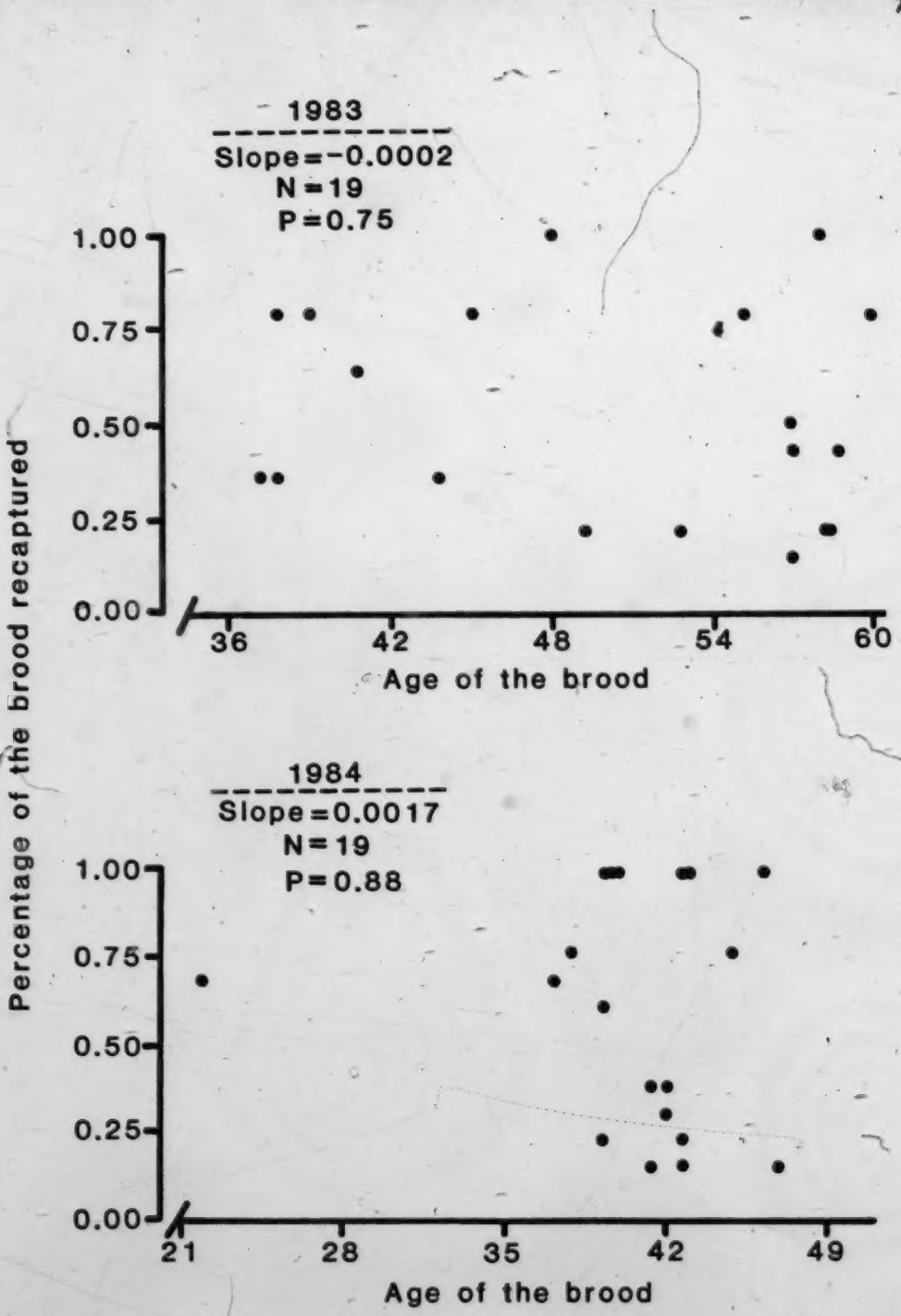

Figure III-3: Relationship between age of the brood in days and percentage of goslings recaptured from broods of Canada geese, in 1983 and 1984 (slope derived from a test for a linear trend in proportion; Snedecor and Cochran 1980).

1979), and great skuas (*Stercorarius skua lonnbergi*) (Williams 1980).

The probability of an egg being fertile is positively correlated with egg mass in domestic turkeys (*Meleagris gallopavo*) (Reinhard and Moran 1979), but in Japanese quail (*Coturnix coturnix japonica*), only very small eggs (< 7.1 g) had a lower fertility rate. Fertilization occurs at the upper end of the oviduct (Sturkie 1976). Thus, if there is any effect of egg size on fertility, it has to be through the size of the ovum. Although it is possible, I suggest that correlations between fertility and egg size are a consequence of maternal effects affecting both fertility and egg size. In other words, a young female may lay a high number of infertile and small eggs.

Another cause of egg failure is embryonic death during incubation. Because energy-rich substances, nutrients, water, and minerals are a necessity for embryonic development (Carey 1983), the quality of an egg can affect the survival of the embryo. Although some egg components are known to vary with egg size (e.g., Ricklefs et al. 1979, Ankney 1980, Ricklefs 1984, Ankney and Johnson 1985, Hochachka 1985), nobody, to my knowledge, has reported any relationships between quality of the egg and embryonic death for wild birds.

For proper development of the embryo, eggs must be maintained within a narrow range of temperatures during incubation. Chicken embryos suffered mortality when exposed continuously to temperatures above 40.5 °C and below 35.0 °C (Lundy 1969, Drent 1973). Even if parents play an important role in maintaining eggs in the proper range of temperature (e.g., Grant 1982, Carey 1983), there are times when eggs are exposed to thermal changes. Large incubated eggs of mallard (*Anas platyrhynchos*) were more resistant (higher percentage of them hatching) to prolonged exposure at 0 °C than small eggs (Batt and Cornwell 1972). These authors also found that embryos in heavy eggs were more likely to survive exposure to temperatures of 0 °C and 8 °C over 10 hours than embryos from light eggs. It takes more time for a large egg to attain the lethal level of temperature because the cooling rate of an egg is negatively correlated with its mass (Frost and Siegfried 1977). The

early nesting habits of the Canada goose could potentially create situations in which embryos are exposed to stressful conditions through low temperatures. However I failed to detect any evidence that small eggs hatched less successfully than large eggs.

This failure to detect an effect of egg size could be because the frequency of egg failure was small to begin with, making it difficult to detect differences. Furthermore, other factors other than size *per se*, such as position of the egg in the nest bowl and the microclimate to which each egg was exposed may have contributed to egg failure. If such an event were to occur, it could mask the effect of egg mass. I concluded that hatchability, a major component of reproductive fitness, was not influenced by egg size in Canada geese nesting at Brooks.

Effect of position in the laying sequence

Hatching success has been related to position in the laying sequence in some species. The first egg of a clutch had poorer hatching success than all other eggs in giant Canada geese (Cooper 1978, Wang 1982). Seven failed eggs were either the last laid or second last laid egg in the hooded crow (Rofstad and Sandvik 1985). The second and the third egg were more successful in producing young than the first or the fourth egg in the shag (*Phalacrocorax aristotelis*) (Snow 1960). In these studies however, the presence of a relationship between egg mass and position in the laying sequence precluded saying which one of these two factors was the most important. In these studies, the positions in the sequence of those eggs which failed to hatch were also associated with low egg masses.

By contrast, Cargill (1979) reported that first eggs were more likely to be preyed upon than eggs later in the sequence in snow geese because predation was heaviest during early laying. She also reported that last eggs were more likely to be abandoned after the rest of the clutch had hatched. Also, position in the laying sequence *per se* may affect hatching success if the timing between copulation and ovulation is inappropriate for complete

fertilization of the clutch. It may also be that if egg quality is associated with position in the laying sequence, some eggs from particular positions are more likely to fail. In this population, however, there was no evidence that position in the laying sequence influenced hatching success. It remains to be demonstrated that position *per se* affects hatching success in precocial species.

Fledging success

Effect of egg size

The potential post hatching survival value of laying an egg of a given size has to be manifested through the size of the gosling, its quantity of reserves, and/or its "quality". In Canada geese, hatching size is highly correlated with egg size (Fig. III-1). This relationship has also been documented in snow geese (*Chen caerulescens*; Ankney 1980), mallards (Rhymer 1982) and pintails (*Anas acuta*; Duncan 1986). Although it was not investigated in this study, the mass of the yolk is positively correlated with the mass of the egg in precocial species like snow geese (Ankney 1980) and Japanese quail (Ricklefs et al. 1978). Therefore, these results suggest that egg size could be under natural selection because it is directly related to hatching size and possibly to the "quality" of the chick.

Many studies of altricial species have shown that chicks from larger eggs survived better to fledging than chicks from smaller eggs (Parsons 1970, Schifferli 1973, Howe 1976, Lundberg and Vaisanen 1979, O'Connor 1979). Controlled experiments with precocial species have also shown higher survival rates for larger chicks (Ankney 1980, Moss et al. 1981, Rhymer 1982). In a natural environment, Cole (1979) showed that in one year larger snow goose goslings survived better than smaller ones. The following year, however, the pattern was reversed, with smaller chicks surviving better than larger ones.

By contrast, others have found no relationship between survival of the chick and egg size: the herring gull (*Larus argentatus*) (Davies' 1975), the kittiwake (*Rissa tridactyla*) (Barrett and Runde 1980), the great skua (Williams

1980), and Canada goose (this study). There are four possible ways to explain my results. First, if the effect of egg size is present but very small, the statistical probability of detecting that effect can be very small (Rotenberry and Wiens 1985). Second, if the environmental selective pressures were low during the 2 years of this study, no differential mortality between chicks from eggs of different sizes would be expected. Third, other factors (yet to be determined) could have masked the effects of egg size on survival. And fourth, egg size does not influence fledging success in this population.

I reject the last explanation because there is considerable evidence that being large at hatching is advantageous. Such advantages include lower metabolic stress per degree drop in temperature (Kendeigh 1969), lower lethal temperature and lower thermal conductance (Rhymer 1982), a more advanced stage of development (Schifferli 1973), and the possession of more body reserves (Marcstrom 1966, Ricklefs et al. 1978). I can not discard any of the remaining explanations, however I can suggest that egg size is not a very important factor influencing fledging success, and hence reproductive fitness in this population of Canada geese. If extreme weather conditions were present, egg size might have influenced significantly fledging success.

Effect of position in the laying sequence

Significant effects of position in the laying sequence have been documented in species showing asynchronous hatching (e.g., Nisbet 1973, Parsons 1970, Howe 1976, Lundberg and Vaisanen 1979, O'Connor 1979). In precocial species, however, hatching usually occurs synchronously (within 12 hours), allowing the entire brood to leave the nest simultaneously. Thus differences in hatching times are small relative to those found in many altricial species. However slight differences in hatching time could be reflected in different levels of awareness in the gosling and also in different degrees of imprinting. Consequently, differential mortality among goslings hatching at different times in the same brood could occur.

Because last laid eggs hatch last (Cooke and Cargill 1981, Syroechkovsky 1975, but see Cooper and Hickin 1972), these eggs are probably the most likely to suffer mortality. Syroechkovsky (1975) found that late-hatched goslings of snow geese were experiencing higher mortality rates than the others of the brood. In his study, however, he also found that last laid eggs were also the smallest eggs. Thus, it is not possible to say whether the mortality was related to the position in the laying sequence and/or the size of the egg. In my study, there was no evidence that position in the laying sequence reflected differences in the potential for reaching fledging age.

Effect of brood size

This parameter can be tested with my data if it is assumed that goslings from all sizes of brood were equally available for recapture. If this system were closed (no emigration and immigration), this assumption would not have to be made because I recaptured almost every bird present, if not all, on the study area. However, overland movements of broods in the area are frequent (Giroux 1980, pers. obs.). In addition, crèching, documented in other populations of the same subspecies (Glasgow 1977), was also observed on my study area. If overland movements and crèching interacted non-randomly with respect to brood size, a potential bias could arise. To produce a significant bias however, broods needed to split up: one part staying in the study area and the remaining part moving out of my study area with a crèche or another brood. On this point, Glasgow (1977) observed that in all cases (N = 7) the entire brood was involved in brood mixing. Although Zicus (1981) has mentioned that "at times, goslings became separated from their parents and broodmates", he did not present data on the frequencies of partial separation of broodmates. Therefore, I felt that this bias was probably too small to affect the results significantly.

My results indicate that every year, the number of goslings per brood near fledging was not related to initial brood size (Table III-3). Andersson and

Eriksson (1982) also found lower production of ducklings for larger broods in common goldeneye (*Bucephala clangula*). However this study should be considered with caution according to Rohwer (1985) because of possible methodological problems. Experimental manipulation of broods in precocial species have led to contradictory results. Safried (1975) found that broods of five chicks in semipalmated sandpipers (*Calidris pusilla*) produced significantly fewer young than the normal broods of four. On the other hand, Rohwer (1985) found that the number of ducklings produced was proportional to the initial brood size in blue-winged teal (*Anas discors*). In other studies in which they compared abnormal brood sizes (crèches) to normal brood sizes, researchers did not detect any differences in survival rates between these two groups (Heusmann 1972, Glasgow 1977, Clawson et al. 1979).

Although it is evident that on my study area large broods did not produce proportionately the same number of goslings that small broods did, the causes are not understood. We know that goslings recorded leaving their parents to join larger broods were not more than 5 days old (Glasgow 1977). Also, the amount of crèching is related to the density of broods in the area (Warhurst and Bookhout 1983). For unknown reasons, larger broods may not have joined other broods as early as smaller broods. Consequently they might have suffered higher mortality because they were not taking advantage of the dilution effect against predation (Munro and Bédard 1977). This explanation is based, however, on the assumption that predation was an important cause of mortality on this area. Although this assumption may be valid, I do not have the data to examine it. Other factors such as relative date of hatching of the brood, overland movements, behaviour of individual parents, and predation may have interacted with brood size to produce this pattern. More studies involving behavioural observations and using radio-telemetry may help to uncover the cause(s) of this phenomenon.

Clutch size of Anserinae is limited by the amount of reserves the females can carry to the breeding grounds at high latitudes (Ryder 1970, Ankney and MacInnes 1978, Raveling 1979). However my results suggest that

in addition brood size may be a factor on which selection can affect clutch size.

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IV. THE RELATIONSHIP BETWEEN SEX OF GOSLING AND POSITION IN THE LAYING SEQUENCE, EGG MASS, HATCHING SIZE, AND FLEDGING SIZE

INTRODUCTION

The possibility that females may be able to control the sex of their offspring has been argued recently in the avian literature (Ankney 1982, Ryder 1983, Weatherhead 1985). Using theoretical arguments, Trivers and Willard (1973) and Myers (1978) showed that it would be adaptive to be able to do so under specific circumstances.

Documented instances in which the sex ratio among offspring varied nonrandomly have been reported for birds. The sex ratio of offspring is reported to vary through the breeding season in red-winged blackbirds (*Agelaius phoeniceus*) (Fiala 1981) and common grackles (*Quiscalus quiscalus*) (Howe 1977). Sex ratio is also reported to vary significantly with position in the laying sequence in snow geese (*Chen caerulescens*) (Ankney 1982, but see Cooke and Harmsen 1983), ring-billed gulls (*Larus delawarensis*) (Ryder 1983), and red-winged blackbirds (Weatherhead 1985). It may be significant that both Fiala (1981) and Weatherhead (1985) only found a significant relationship in four-egg clutches but not in three-egg clutches.

To investigate this phenomenon in Canada geese (*Branta canadensis*), I studied the relationship between the sex of a gosling and four variables: position in the laying sequence, egg mass, hatching size, and fledging size.

STUDY AREA AND METHODS

The data were obtained in 1983 and 1984 near Brooks (50° 35'N, 111° 54'W), Alberta (Fig. II-1). They were collected in two different ways. The first source of data was from a wild population nesting at Gleddie Lake. From late March to late April, I searched this reservoir daily in 1983 and every 2 days in 1984 for nests. Upon discovery of a nest, each egg was marked with a waterproof felt pen with the date of discovery. Nearly all nests had one or two eggs when found, although some had three. The

degree of staining of eggs was used to assess the order of laying (Cooper 1978). The sequential position of the remaining eggs in the clutch were determined by subsequent visits during the laying period. In this study, I excluded nests that were found with more than three eggs and nests in which the order of laying could not be assessed with absolute certainty for the two or three eggs. Fresh mass, maximum length and breadth were determined for each egg.

During pipping, embryos were web-tagged following the technique of Alliston (1975). On several occasions, I visited the same nest twice during the pipping-hatching period and was able to determine the sex by cloacal examination of every gosling in the nest in some cases. In late June and early July, I conducted banding drives in the area to recapture marked goslings. At the time of round-up, goslings were 5 to 8 weeks old. Upon recapture each gosling was weighed, and the lengths of its culmen and tarsus recorded. I also determined the sex and checked for the presence of a web-tag on each individual recaptured.

The second source of data was from six other reservoirs in 1984: Tilley "A", Tilley "B", Rolling Hills Lake, Kininvie Flat, and Cowoki Lake (Fig. II-1). I used the same procedure as outlined for Gleddie Lake up to the week 3 of incubation. At that time, all six-egg clutches with known laying sequence were removed from their nests and the eggs were hatched in an artificial incubator at the Brooks Wildlife Center, Alberta. Clutches of six eggs were used because they were the most common on the study area. Prior to hatching, each egg was individually isolated in the incubator to associate each gosling with its position in the laying sequence. Within 4 hours of hatching, each gosling was web-tagged in the left foot with an individually-numbered metal tag. At this time, they were also weighed to the nearest 0.1 g using a Sartorius scale. I determined the sex of each individual 24 hours after replacing them into the incubator where they were allowed to dry. All eggs that did not hatch were noted and their position in the laying sequence recorded.

Contingency tables were analysed using G-tests (Sokal and Rohlf 1981). Covariance analysis were done using the BMDP computer package (Dixon et al. 1983).

RESULTS

Position in the laying sequence

The relationship between sex ratio and laying sequence was studied with two different sets of data: first with the marked and recaptured data at Gleddie Lake, second with artificially hatched eggs. In the first set, I examined only goslings from nests with original clutch sizes of five and six eggs. These sizes were the most common on the study area. For both clutch sizes, there was no correlation between sex of the gosling and position in the laying sequence (Table IV-1 and Table IV-2). Furthermore, the overall sex ratio among goslings from clutches of both five and six did not differ from unity (five-egg clutches: $X^2 = 1.88$, df = 1, P = 0.17; six-egg clutches: $X^2 = 2.63$, df = 1, P = 0.10). In this data set, however, the sex was determined 5 to 8 weeks after hatching. Using this method, sex was determined for only 49% of the goslings that actually hatched. It is therefore possible that differential mortality between sexes during the first 5 to 8 weeks may have masked differences in sex ratio present at hatching. Thus, in 1984 I determined at hatching the sex of 242 goslings from 44 six-egg clutches. As with the recaptured goslings, there was no significant association between sex and position in the laying sequence (Table IV-3). The overall sex ratio of offspring also did not differ from unity ($X^2 = 1.65$, df = 1, P = 0.20). The sex of the embryo in every egg laid was not known because some eggs (22/264) were either apparently infertile or the embryo had died early in its development. Nevertheless these results strongly suggest that there is random segregation of sex within a clutch.

TABLE IV-1: Sex of Canada goose goslings determined at 6 to 8 weeks old from sequentially-laid eggs in five-egg clutches (N = 14), 1983 and 1984 combined.

	Egg sequence					
Sex	1	2	3	4	5	Total
Male	3	5	3	6	4	21
Female	3	4	4	1	1	13
Total	6	9	7	7	5	34

G-test; G = 4.244, DF = 4, P = 0.37

TABLE IV-2: Sex of Canada goose goslings determined at 6 to 8 weeks old from sequentially-laid eggs in six-egg clutches (N = 13), 1983 and 1984 combined.

	Egg sequence						
Sex	1	2	3	4	5	6	Total
Male	5	6	4	4	5	0	24
Female	3	1	3	2	4	1	14
Total	8	7	7	6	9	1	38

G-test; G = 4.126, DF = 5, P = 0.53

TABLE IV-3: Sex of Canada goose goslings determined at hatching from sequentially-laid eggs in six-egg clutches (N = 44).

	Egg sequence						
Sex	1	2	3	4	5	6	Total
Male	21	22	20	27	23	18	131
Female	22	15	19	15	20	20	111
Total	43	37	39	42	43	38	242

G-test; G = 3.518, DF = 5, P = 0.62

Egg mass, hatching size, and fledging size

Egg mass varies within clutches of Canada geese (Chapter II). Mass of the egg is also correlated with hatching mass of the gosling. Therefore the possibility exists that a female can provide different amounts of parental investment to a male or a female offspring by selecting specific sizes for one particular sex. However, in six-egg clutches for which the sex of the goslings was known at hatching, no differences were found between the mass of eggs from which males and females hatched for all positions in the sequence (Table IV-4). Within clutches there was no difference between the mean egg mass of males and females (paired t-test; $t = 0.14$, $df = 40$, $P = 0.89$). The mass of males and females at hatching neither differed within positions in the laying sequence (Table IV-5), nor within a clutch (paired t-test; $t = 0.35$, $df = 32$, $P = 0.73$). There was an exception for the fifth egg; males were smaller than females. I do not believe that this exception represents a real pattern since in all other positions, there was great similarity in the size of males and females. In a random sample of goslings from 36 eggs (only one *per* clutch), there were no differences in either culmen length (t-test; $t = 1.78$, $df = 34$, $P = 0.083$) or tarsal length (t-test; $t = 0.02$, $df = 34$, $P = 0.986$) between newly hatched male and female goslings.

Although no differences in hatching size were present between males and females at hatching, body mass of males was 16% and 8% higher than females near fledging in 1983 and 1984 respectively (Table IV-6 and Table IV-7). The difference was smaller in 1984 probably because goslings were recaptured 2 weeks earlier than in 1983. Tarsi of males were also significantly longer than those of females near fledging in both years of study (Table IV-6 and Table IV-7). Culmen lengths were not different between males and females at this stage of development in either years.

TABLE IV-4: Mean (±SD) egg mass (g) by sex and laying sequence in six-egg clutches.

Sex	Egg sequence					
	1	2	3	4	5	6
Male	158.9±9.7 (21)[1]	163.9±8.9 (22)	168.0±10.5 (20)	167.8±10.6 (27)	160.8±9.6 (23)	154.4±7.4 (18)
Female	160.1±12.9 (22)	165.3±9.6 (15)	166.7±8.7 (19)	165.9±8.6 (15)	165.6±11.8 (20)	160.3±12.6 (20)
Difference[2]	0.34	0.48	0.41	0.49	1.48	1.71
P[3]	0.74	0.64	0.68	0.63	0.15	0.10

[1] Number of eggs in parentheses
[2] Value of t based on a Student's t-test between sexes
[3] Probability level

TABLE IV-5: Mean (±SD) hatching mass (g) of goslings by sex and laying sequence from six-egg clutches.

	Egg sequence					
Sex	1	2	3	4	5	6
Male	104.3±7.0 (14)[1]	110.5±6.4 (17)	113.8±9.0 (14)	113.8±7.8 (16)	105.3±6.0 (15)	103.5±4.9 (14)
Female	106.4±9.8 (18)	110.8±7.7 (10)	111.7±6.7 (13)	110.1±5.7 (14)	113.8±8.5 (15)	105.4±7.8 (15)
Difference[2]	0.69	0.13	0.67	1.48	3.16	0.78
P[3]	0.50	0.90	0.51	0.15	0.00	0.44

[1] Number of goslings in parentheses
[2] Value of t based on a Student's t-test between sexes
[3] Probability level

TABLE IV-6: Analysis of covariance on the relationship between size and age for male and female Canada goose goslings near fledging in 1983.

	N	Mean age (days)	Adjusted group mean		
			Body mass (kg)	Tarsal length (mm)	Culmen length (mm)
Male	28	50.0	2.36	108.7	42.8
Female	17	50.5	2.03	103.0	41.8
F[1]	--	---	14.064	13.604	1.173
P	--	---	0.0005	0.0006	0.29

[1] Based on a F-test for equality of adjusted means between male and female (values given are F values plus probability level for difference between male and female)

TABLE IV-7: Analysis of covariance on the relationship between size and age for male and female Canada goose goslings near fledging in 1984.

	N	Mean age (days)	Adjusted group mean		
			Body mass (kg)	Tarsal length (mm)	Culmen length (mm)
Male	29	40.5	1.89	106.8	40.5
Female	20	41.3	1.75	100.5	39.5
F[1]	--	---	7.220	17.535	3.228
P	--	---	0.01	0.0001	0.079

[1] Based on a F-test for equality of adjusted means between male and female (values given are F values plus probability level for difference between male and female)

DISCUSSION

The relative value of each sex of young to the fitness of the parents may vary with the sex ratio of the breeding population and also with the "costs" of producing each sex (Maynard Smith 1984). If values differ between sexes, one would expect differences in the parental investment for each sex.

There is a difference in parental investment associated with the laying sequence in Canada geese (Chapter II). Therefore theoretically, it may be advantageous to produce one sex at a particular position in the laying sequence if it can affect the survival to reproductive age of the offspring. However, there was no evidence of such a phenomenon in the population of Canada geese studied. These results agree with those recorded by Cooke and Harmsen (1983) who studied snow geese. Fiala (1981) and Weatherhead (1985) both found significant relationships between sex ratio and position in the laying sequence in four-egg clutches but not in three-egg clutches of red-winged blackbirds. In four-egg clutches however the patterns obtained were opposite; Weatherhead (1985) found that last laid eggs produced more males while Fiala (1981) recorded more females for last laid eggs. Caution should be applied to Fiala's results because he determined sex 8 days or more after hatching. Thus, his results could be explained by male biased mortality in the immediate post-hatch period. These two studies do not add much weight to the claim that females can control the sex of their offspring because significant relationships were found only in four-egg clutches but not in three-egg clutches. Moreover, these two studies reported opposite relationships in the same species.

In contrast, Ankney (1980) and Ryder (1983) documented significant relationships between sex ratio at hatching and position in the laying sequence in snow geese and in ring-billed gulls respectively. In these two studies however the effect of this relationship on the reproductive success of sons and daughters is not known. Therefore it is very difficult to say if it has an adaptive value (Clutton-Brock 1982).

Again if one sex is more valuable to parents than the other, they should invest more in that sex to make sure that it survives to reproductive age. My results suggest that from laying to hatching there is no evidence that females invest more in one sex than the other. Egg mass and hatching size were essentially the same for males and females. Ankney (1980) also found no differences in these parameters among snow geese. In his study, however, female goslings had a slightly shorter culmen than males. Near fledging, however, body mass and tarsus length were greater in males than females in both snow (Ankney 1980) and Canada geese (this study) It is apparent that males must grow faster than females between hatching and the date of recapture. These differences between males and females at fledging are unlikely to be the result of differences in parental care, because parents do not feed their young. Thus, there is very little opportunity to control feeding rates of goslings of a given sex. Moreover, during the rearing period, broods mix and form crèches with up to 80 goslings (Glasgow 1977, Zicus 1981, pers. obs.). In these crèches, only a few pairs remain with the gang making it very difficult to provide more parental care to one sex than the other. Ankney (1980) showed that, without parents, female goslings grew at a lower rate than males. It is then evident that the difference between male and female goslings near fledging is not the result of different amounts of parental care provided to either one sex or the other.

Ankney (1980) suggested that females were investing slightly more in their male offspring by producing males in the two first and larger eggs of the clutch. My data did not show this phenomenon, and moreover, parental investment in male and female goslings did not differ up to hatching and possibly up to fledging. To conclude, my study suggests that male and female goslings are equally valuable to Canada geese parents because parental investment appears to be the same for each sex.

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V. CONCLUDING DISCUSSION

Examination of eggs produced by Canada geese (*Branta canadensis*) nesting at mid latitudes revealed that egg size is not "relatively constant" as Lack (1967) suggested for this and any other species of Anatidae. Most of the variation (two-thirds of the total variance) in egg size exists among females, the remainder from among eggs of the same clutch.

Variation of egg size among females does not appear to be influenced by environmental factors other than those affecting the body condition of the female. Even if body condition is the only factor found to be correlated significantly with egg size, it explained a very small part (14%) of the variance of mean egg size among females. On the other hand, genetic differences among females could explain most of the variation observed. This suggestion is based on three facts. First, captive females were very consistent in mean egg size between clutches laid the same year and in two different years. Second, other studies based on repeatability (e.g., Batt and Prince 1978, Moss and Watson 1982, Nol et al. 1984) and heritability estimates (van Noordwijk et al. 1981) suggest strongly that egg size is relatively fixed genetically. Third, percentages of the total variance accounted by differences among females and within clutches were very similar in the wild and in captivity.

The presence of this variation and its possible underlining genetic basis in egg size is the raw material upon which natural selection can act. However, evolutionary changes can only occur if there are some selective advantages to laying eggs of a certain size. In my study, however, I found no evidence, within the normal range of variation, that egg size influenced the reproductive success of female Canada geese. Therefore, I suggest that differences in egg size among females have a very limited influence on fitness. I used the term "limited" because phenotypes that laid eggs of a size below or above the normal range, would probably have a reduced fitness. Nevertheless, egg size may become an important component of fitness if environmental conditions were to change significantly during critical periods between laying and fledging. Hypothetically, if such changes affected the food

abundance and induced severe cold stress, larger eggs and goslings would probably be favoured for various reasons (see Batt and Cornell 1972, Ankney 1980, Rhymer 1982).

Variation of egg size within clutches of Canada geese followed a curvilinear pattern in which eggs in the middle were very similar in size, yet larger than the first and last eggs in the sequence. The adaptive significance of this source of variation for altricial species showing asynchronous hatching has been discussed mainly in relation to the brood reduction strategy and predation (see Slagsvold et al. 1984).

However, for a species like the Canada goose, two aspects of its life history make it very different from an altricial species. First, hatching within a clutch occurs synchronously or almost so. Second, the parents do not feed their young. Therefore, any patterns of variation that could favor brood reduction (e.g., Howe 1976) is probably inapplicable to this species. However, this pattern could be adaptive if, between eggs of different positions, there were differences in the likelihood of producing a gosling that reached reproductive age. On this point, I found in this study that eggs in different positions in the laying sequence were equally likely to hatch and to produce a gosling that reaches fledging age. These results differed from those of Cooper (1978) and Cargill (1979) in which some eggs (first and last laid) were less likely to produce chicks that reach fledging age because of partial predation on the clutch, abandonment of eggs, and/or infertility. Selective pressures on my study area might not have been as intense as on theirs. Therefore, I propose that the pattern of variation within clutches reflected the direct effects of physiological changes in the reproductive tract on eggs during their formation. This hypothesis needs to be examined more thoroughly and the direct causes uncovered.

The variation in egg size with laying sequence was suggested as a way in which a female could direct her parental investment to one sex of offspring in particular, by controlling the sex of her young in relation to the laying sequence (Ankney 1982). In this study, I found no evidence that female

Canada geese were able to control the sex of their offspring in relation to laying sequence. Moreover, parental investment did not differ between male and female goslings at least up to hatching and possibly up to fledging age.

In addition to egg size, initial brood size did not influence the reproductive success of Canada geese nesting at Gleddie Lake. Thus, females producing different sizes of brood had approximately the same apparent fitness. The reasons for this remain unknown but overland movements, crèching behaviour, and relative date of hatching may play an important role. These results are interesting because the influence of brood size was measured using sizes of normal broods as opposed to other studies (e.g., Safriel 1975, Rohwer 1985) that used abnormal brood sizes. It suggests that brood size may not be an important component of fitness at least within the normal range of brood sizes.

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